ICES CM 2009/E:5

Climatic Impact on Northeast Arctic Cod Year-class Strength: Relevance to the Ricker and Beverton-Holt Models for Determination of the Recruitment-stock Dependence

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Abstract

Integral quantitative assessment of the environmental impact on the NEA cod year-class strength has been made with use of the survival index. Three types of survival conditions with different impact of spawning stock on recruit abundance were difined. There is a significant correlation between the survival index and the spawning stock, the recruitment abundance (40,1%), the water temperature (R=55,1 under p<0,01), the North Atlantic Oscillation (NAO) index, and the pressure gradient above the Barents Sea which allows us to use the survival index as an indicator in the year-class strength. These relationships allow to develop the forecasting sistem for abundance of future year-classes. It is shown that the Ricker and Beverton-Holt models are not appropriate for determination of the recruitment-stock dependence for NEA cod.

Key-words: survival index, Northeast Arctic (NEA) cod, variability in the year-class strength, climatic variability, temperature water, the NAO index, the pressure gradient, the Barents Sea

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Introduction

Highly productive marine ecosystems are characterized by a great temporal (interannual, decadal, and long-term) variability in productivity of waters and abundance of fish stocks, which could be associated with a significant impact of physical stresses on processes of formation of these properties. Dynamics of the fish stock abundance in these ecosystems is determined by the year-class strength, while the latter depends on abundance of the spawning stock, environmental conditions (biotic and abiotic) which influence both the productive condition of spawners, quality of eggs, and survival and growth of a new generation. Given significant variability and interdependence of these parameters in highly productive marine ecosystems, forecasting of variations in year-classes and future state of the fish stock should be essential part of the fishery management.

At present forecasting is based either on mathematical models build round the stock-recruitment system, or empirical quantitative relationships and dependences between principal parameters which regulate the recruitment dynamics. Thus it is possible to use correlations to compute abundance of future generations.

In this work, we have made an attempt to achieve two goals. Firstly, based on the retrospective analysis of survival indices of the NEA cod year-classes during the period of 1946-2002, examine qualitative and quantitative impact of the survival conditions on abundance of year-classes. Secondly, to estimate abundance of year-classes with conventional models introduced by Ricker (1954) and Beverton-Holt (1957) and compare the results with observed values in order to decide whether these models are efficient forecasting tools.

Material and methods

The principal material of our study is the analysis of long-term data (1946-2002) on the spawning stock biomass and the year-classes abundance of the NEA cod at age 3, which were submitted to the ICES WG on the Arctic fisheries (Anon, 2002). We assumed the abundance of generations at age 3 as the "observed abundance". Its values were computed with the virtual population model and its modifications.

The data are summarized in Table 1 which presents survival indices (*SI*). Survival indices (*SI*) are a ratio between the abundance of the year-class at the age of 3 (R_{3i}) and the biomass of the spawning stock (BR_{3i}) in the year of appearance of generation *i* and are presented as a number of survived fish per 1 tonne of the spawning stock or survived fish per 10^6 eggs:

$$SR_i = R_{3i} / BR_{3i} \quad (1)$$

Dependence of the year-class abundance dispersion on the spawning stock is found with the single-factor dispersion analysis (Table 2). Similarly, we assessed the dependence of the generation abundance on survival factor as indicators of the physical conditions of the year-class abundance formation (Table 3). Table 4 summarizes reproductive parameters of the population.

Objective clusters of the cod year-class survival indices were selected in the long-term set of observations with the method of minimal dispersion (Ward, 1963). Analysis and computations were made with the Statgraf software.

Relationship of the survival indices with the temperature regime in the Barents Sea was analyzed using the mean annual water temperature anomalies in the layer of 0-200 m at the Kola section. The temperature conditions of survival were determined as an averaged weighted sum (T_{aw}) of the mean annual water temperature anomalies over four years: the pre-spawning year (because it determines the reproduction capacity of the spawning stock) (T_{i-1}), the spawning year ($2*T_i$), the first ($2*T_{i+1}$) and the second (T_{i+2}) years after spawning: $T_s = (T_{i-1} + (2* T_i) + (2* T_{i+1} + T_{i+2}))/6$ (2).

Identifying dependence of the survival indices on wind conditions, we applied values of the NAO mean winter (December-March) index. For convenience of comparison with the physical characteristics, the survival indices were expressed as natural logarithms of the ratio between the generation abundance and the spawning stock biomass. All the data here are given for the year of spawning.

To identify relationship of the survival rates with the temperature and wind conditions we used the standard statistical software.

Retrospective computations of the year-class abundance (Table 5) were done with Ricker's two formulas (1979) and four modifications of the Beverton-Holt models (1957) introduced by Hilborn and Walters (Hilborn, Walters, 1992).

Ricker's first formula which can be applied independently of what units recruitment and spawning stock are expressed in is as follows:

$$\mathbf{R = \alpha P e^{-\beta P}} \quad (3)$$

Where:
R is the number of recruits; P is the abundance of spawning stock a; α is the non-dimensional parameter; β is the1/P dimension parameter.

Ricker's second formula. Ricker's simple equation (3) can be transformed as it is done by Brander and Mohn (Brander, Mohn, 2004) and parameters α and β can be expressed in more natural units as maxima on the assumed curve, i.e. as the maximum biomass of the spawning stock (SSB_{max}), and the maximum recruitment (R_{max}):

$$\mathbf{R = exp(Rmax/SSBmax)\ SSB\ exp(-SSB/SSBmax)} \quad (4)$$

Computations with the Beverton-Holt model. The main equation of Beverton and Holt (Beverton, Holt, 1957), which describes the curve of the recruitment dependence on the stock, is as follows:

$$\mathbf{R = aS/(b + S)} \quad (5)$$

Where:
R is the recruits (in our case this is the recruitment abundance at age 3); S is the biomass of the spawning stock (SSB); *a* is the mortality coefficient independent on the population density and *b* is the mortality coefficient which depends on the population density.

There are four ways to determine parameters *a* and *b*.

1. In formula (4) *a*, according to Hilborn and Walters (1992), is the minimum abundance of recruits and *b* is computed for each year with the help of the transformed formula (4):

$$S/R = b/a + S/a \qquad (6)$$

2. In formula (5) *b* is the spawning stock necessary to produce generation with abundance of *a*/2, *a* is computed for each year with formula (3).
Mean long-term *a* is used to compute R with formula (5).

3. The maximum abundance of recruits (*a*) is found with the first method, while *b,* i.e. the spawning stock necessary to produce generation with abundance of *a*/2, is determined with the second method.

4. We transform equation (5) as follows:

$$\log(R) = \log aS/b+S \ \pm w, \qquad (7)$$

where *a* and *b* are computed with the help of the nonlinear regression, dispersion *w* is the dispersion of the remainder (δ^2). The year-class abundance is found with the following formula

$$R = \frac{aS}{b+S}\exp(\delta^2/2) \qquad (7.1)$$

Results

Clustering of the survival indices and qualitative and quantitative assessment of the environmental impact on the year-class abundance

The problem of how to express the environmental impact on the year-class survival has always been vital. The generation abundance bears the mark of influence produced by two factors, the spawning stock and conditions of survival and growth.

Survival index expressed as a relationship between abundance of organisms which survive until a particular age (in case of cod it is three years) and the total amount of produced eggs could be used as an indicator of the habitat quality (Radovich, 1962; Beverton, 1962; Bondarenko et al., 2003, 2008; Ponomarenko, 1996; Serebryakov, 1990; Serebryakov, Chumakov, 1992; Serebrykov et al., 1983; Shelton et al., 2003).

According to our estimates, in 1946 – 2002, survival indices of the cod year-class 3 changed from 0.78 to 25.28 per 10^6 eggs, with mean values 6.50 per 10^6 eggs.

Figure 1 shows the main peculiarities of the impact produced on the reproduction success by environmental conditions and the biological factors. Peaks of the cod survival indices coincide with high values of the year-class abundance. The highest values of the cod survival indices and the generation abundance are associated with years when the spawning stock was minimum. Years of large spawning stocks are often characterized by low abundance of year-classes and survival indices. However, in some years of large spawning stocks there were high values of the year-class abundance, but low values of survival indices. There are no apparent direct correlation between the reproduction success and the physical conditions of survival, i.e. anomalies of the sea water temperature and wind conditions.

In order to quantitatively characterize these and other peculiarities of impact which the physical and biological conditions of survival make on the reproduction success, we have undertaken clustering of the survival indices and identified three types of the survival conditions (Tables 6, 7, and 8): favorable, moderate and unfavorable.

There were 9 year-classes born in favorable conditions (16.1 %), 15 year-classes were born under moderate conditions (26.8 %), and 32 year-classes appeared in years of unfavorable conditions (57.1 %). Such ratio of year-classes shows that in more than half cases the cod population was under the stress conditions, caused by impact of the biological and physical factors.

Under favorable conditions of survival (tables 6), the mean value of the spawning stock was very low totaling 204,000 t (142 - 327,000 t), while the generation abundance was great: six strong year-classes and three middle year-classes (638 – 789 x 10^6). It is likely that in years of favorable conditions of survival there is a sharp decrease in negative impact of cannibalism on the part of elder cod because it is few. For example, Ponomarenko (1996) and Ponomarenko & Yaragina (1984) showed that cannibalism influenced the reproduction success. Mehl, Tjelmeland (1990) also consider cannibalism to be a of compensatory mortality.

From nine generations, four (1963, 1964, 1969, 1970) with the greatest survival rates (19 – 25 per 10^6 eggs) appeared in years of the negative NAO mean winter index (from -0.53 to -2.09). This points to the fact that these year-classes were particularly influenced by wind conditions during the spawning period, as well as during the consecutive drift of the cod eggs, larvae and the 0-group (Fig. 2). Other generations had survival indices 1.5-2 times less (10 – 14 per 10^6 eggs). They appeared under the positive NAO mean winter index (1.16 – 2.86) and one year-class appeared under a low negative NAO mean winter index (-0.27) which happened in 1958. These data indicate necessity of taking wind conditions into account in forecasting abundance of future generations.

In numerous publications (Borisov et al., 2006, etc.) it was noticed that strong year-classes appear in warm and cold years. Indeed, the mean annual water temperature in the layer of 0-200 м (the Kola section) in 1963 and in 1969 годах could be named very cold (3.40 and 3.68^0 C) (Izhevskiy, 1961, 1964). However, these years were characterized by great abundance of year-classes and high survival rates (24.871 and 19.110, per 10^6 eggs, respectively). Two very strong year-classes (1964 and 1970) appeared in warm years (4.08^0 C and 4.15^0 C). From the rest five generations three appeared in very warm years (1975, 1983, 1989), one year-class (1957) occurred in warm year, and another one – in a cold year (1958). Therefore, forecasting the reproduction success, we should consider the temperature regime rather for the entire period of the generation development, than for the spawning year.

Under the moderate survival conditions, mean values of the cod year-class abundance at age 3 decreased down to 611 x 10^6ind., however, correlation between the minimum and maximum abundance increased up to 1:6 against 1:3

(under favorable conditions). In years with moderate conditions of survival there was one strong year-class (1950), nine middle and five poor year-classes. The mean value of the survival indices dropped down to 6.9 per 10^6 eggs(against 16.9 per 10^6 eggs under favorable conditions). The variation range of the survival indices narrowed to 5- 8 x10^6 eggs. The spawning stock was in the range from 118,000 t - 615,000 t with the mean value of 294,000 t. Spawners with biomass below 350,000 t produced 13 generations, five of which had biomass below 230,000 t. The lowest survival indices occurred in years when the stock biomass exceeded the mean value (326,000 t; 430,000 t, and 615,000 t).

Under moderate conditions of survival, the minimum abundance of year-classes (<470 x 10^6ind.) were in years when the spawning stock biomass was below 230,000 t (1968, 1974, 1981, 1987, 1988, 2000). Physical conditions were characterized by the positive NAO mean winter index and four very cold years. The maximum recruitment (1590 x10^6ind.) occurred in 1950; it was produced by the spawning stock with biomass of 675,000 t under the positive NAO mean winter index and in a very warm year.

The year-class abundance in the range from 680 – 805 10^6ind. characterized four years, i.e. 1954, 1956, 1962, 1990. Two of these generations were produced by the spawning stock with biomass of 300,000 t and 312,000 t in years of the negative NAO mean winter index (-0.80 – 0.57); one generation appeared in a very cold year and the other – in a very warm year. The rest two were produced under the positive NAO mean winter index and in very warm years.

Under unfavorable conditions of survival we identified 32 year-classes. In this group, we should highlight the following mean values of the principal indicators: the spawning stock – 435,000 t (102 – 1165,000 t 1:10) and the year-class abundance – 399 x 10^6ind. (112 – 1193 x 10^6ind., 1:10).

The physical factors were characterized also by maximum variations: the NAO mean winter index varied in the range from 2.32 - 2.44, the mean annual sea water temperature was 2.83 – 4.60^0 C. In this group, 15 years were cold or very cold. The weakest year-classes appeared in years of low spawning stock and cold temperatures (1965, 1966, 1967, 1976, 1978, 1979, 1980, 1984, 1985, 1986).

From years when the spawning stock was large (730,000 t – 1165,000 t) four years showed low survival idices (0.776 – 1.417 per 10^6 eggs). As to the year-class abundance, it was below the mean value in 1992 and in 1993 and above the mean in 1946 and 1947. In 1948 and 1949, strong year-classes appeared (1,083 – 1,193 x 10^6ind.), however, their survival indices were the lowest (0.776-1.082 per 10^6 eggs). In all years when the spawning stock was large (except the cold 1948), temperature conditions were favorable for survival. The NAO mean winter index was negative in 1947 (i.e. favorable for survival) and positive in other years. The fact that the spawning stocks of large biomass did not produce abundant generations which would correspond to their fecundity is likely to be the result of the negative impact of both wind conditions, and cannibalism of the NEA cod.

The impact of the survival indices on variability in the abundance of cod at the age of 3 made 40.1% (Table 3).

The cluster analysis allowed for the statistical determination of the spawning stock role (Table 4) which appeared to be insignificant (1.1%).

The statistical analysis of the SSB role in the abundance variability for the cod year-class 3 in three groups revealed (Tables 9, 10, and 11) that under unfavorable conditions of survival, this role made 37.2%, while under moderate conditions it could be 91.9%, and under favorable conditions - 16.3%, however, this value is statistically insignificant.

The analysis allowed us to present the NEA cod reproductive parameters as follows (Table 4). The spawning stock with the mean biomass of 374,000t (and the variation range from 102,000 t - 1165,000 t) corresponded to the mean fecundity of 133 x 10^{12} eggs (33 – 651 x 10^{12} eggs) and the mean year-class abundance of 565 x 10^6ind. (112 – 1818 x 10^6 ind.). Strong year-classes appeared when survival indices varied from 2 - 25 per 10^6 eggs, middle difference year-classes correspondent to survival index in the range from 0.78 - 14.4 per 10^6 eggs, and poor year-classes were associated with survival indices 1.31 - 8.49 per 10^6 eggs.

The accomplished analysis of the NEA cod year-class 3 survival index by three types of survival conditions allows us to conclude that there is a certain critical level of the spawning stock biomass. The critical biomass of the spawning stock is the biomass of spawners which could only produce a highly abundant generation under maximum favorable conditions of survival of eggs, larvae and young fish, but already under moderate conditions of survival there would be no chance for appearance of a moderately abundant generation. When the reproductive fecundity of the fish population would decrease below this critical level, appearance of strong year-classes in such population becomes statistically unlikely. During the entire period of observations the cod SSB was close or below the critical level (106,000 t) twice, in 1965 and 1980, when the spawning stock biomass totaled 102,000 t and 108,000 t, respectively. Despite mean survival indices (4.52-4.75 per 10^6 eggs), the produced recruitment was extremely poor (165-167 per 10^6 ind.) (Bondarenko et al., 2003).

Relationship between the survival rates and the temperature regime

Marine biologists have already identified general regularities of the temperature impact on survivability of young generations for various fish species. It is known that strong year-classes of Norwegian spring-spawning herring, Northeast Arctic cod, and Northeast haddock tend to appear in years when the mean annual or seasonal temperature at the Kola meridian exceeds the long-term values (Izhevskiy, 1961, 1964; Hjermann et al.,2004; Mikkelsen, Pedersen, 2004; Saetre et al., 2002 et al.).

Elevated temperature, according to Gulland (1965), Ware (1975), and Satrapa (1996), stimulates the fish growth. Growth rates increase due to intensification of the fish feeding and metabolism. Elevated temperature is also favorable for development of zooplankton and, consequently, for availability of food stocks for larvae (Nesterova, 1990; Ottersen, Loeng, 2000). Higher growth rates increase survivability because larvae and young fish become more capable of escaping predators.

Temperature regime in the Norwegian and Barents seas depends on the heat transfer from southern latitudes, particularly it depends on the Gulf Stream with its northern extensions (Izhevskiy 1961, 1964). This transfer is influenced by tidal events, as well as advection of the temperature anomalies by currents (Sutton, Allen, 1997). All this results in a high variability in the temperature regime on the interannual, decadal, and long-term scales. There is a relationship between this variability and variations in strength of the cod year-classes (Satersdal, Loeng, 1987; Borisov, Elizarov, 1989, Drinkwater, 2005; Mikkelsen, Pedersen, 2004).

However, despite a significant impact of water temperature on NEA cod survival, we cannot state that there is a direct dependence of the successful formation of abundant generations of the commercial fish species on the type of the temperature regime in the year of the generation appearance (Borisov et al., 2006; Toresen, Ostvedt, 2000; Stein, Borovkov, 2004; Ottersen, Loeng, 2000). Thus, Borisov et al. (2006) emphasizes that strong year-classes appear both in "warm" and in "cold" years. Similarly, poor year-classes were also registered both in "cold" and in "warm" years. This could be explained by the fact that marine scientists did not consider the temporal scale of the temperature impact on all the successive stages in the fish life cycle, from the spawners' maturation stage till recruitment of the new generation into the fish stock. Therefore, comparison of temperature conditions with the earliest stages of life cycle (only one year of life) cannot be a direct indicator of survival.

At VNIRO we have made a comparative analysis of the temperature variations during four years of life of one generation of NEA cod and its survival index at the age of 3 (Krovnin, personal communication). Data presented in Fig. 2 demonstrate a rather strong positive correlation ($R=0,56$, $p < 0,01$) between the survival index and the integrated thermal conditions which determine strength of the given year-class.

Relationship between the survival rates and the atmospheric circulation (wind conditions)

The index of the North Atlantic Oscillation (NAO) is characterized the sea level pressure (SLP) difference between the Icelandic Low and the Azores High. There is a close link between the mean winter (December-march) NAO index variability and associated interannual and decadal variations in sea and air surface temperatures in the North Atlantic, sea level pressure, and surface winds (Marshall et al., 2001).

As seen from Table 12, the favorable survival conditions for cod were observed both in years with positive and negative values of the mean winter NAO index. However, the values of survival index in years of the positive NAO index were by 1.5-2 times lower than in years of the negative NAO phase. Generally, the favorable conditions for cod survival are formed in years with weak SLP gradient with prevalence of weak anomalous north and northeast winds over the Barents Sea Fig.3). This situation favors the accumulation and growth of cod juveniles in the southwestern Barents Sea.

The unfavorable survival conditions are also observed both in years with negative and positive values of the NAO index (Table 12). But, in this case, Icelandic Low and Azores High are shifted eastward from their mean long-term position, with formation of the high-gradient baric zone over the sea and predominance of strong anomalous east or northwest winds (Fig. 4,5).

Thus, the year-class strength of NEA cod is affected not only by advection of warm Atlantic waters with the North Atlantic current system but by the value of atmospheric pressure gradient over the Barents Sea also.

On possibility of forecasting recruitment on the basis of qualitative and quantitative relationships between the survival indices and the year-class abundance

The first successful forecasts of the NEA cod stock dynamics 5-6 years in advance were made by Izevsky already in 1961 and 1964. These forecasts were based on the significant correlation between catches per 1 hour of trawling and the mean annual temperature in the layer of 0-200 m at the Kola section (Izhevsky, 1961, 1964). He forecasted the mean annual water temperature considering three types of quasi-periodical variations in the heat advection into the Barents Sea: 4-6, 8-10, and 18-20 years. It was Izhevsky who forecasted that in 1970 the heat content in the sea would reach its high level due to imposition of peaks in variations in these years. It is known that for the entire observation period, 1970 became the year when the smallest spawning stock of cod (224,000 t) produced the most abundant generation (1818×10^6 ind.), which was supported by a high negative value of the NAO mean winter index (Table 6).

The modern technological advances in the cod fishery make use of the CPUE indicator almost impossible. Besides, the fisheries statistics is not often reliable and it is difficult to consider discards. In the 1950s-1960s marine scientists did not encounter such problems.

The application of the Izhevsky technique in forecasting of the mean annual temperature in the layer of 0-200 m at the Kola section allows us to use the thermal regime as the initial basis for forecasting of the cod survival index three and more years in advance. Moreover, we could use dynamic and statistic models (Marshal et al., 2001, Rodionov and Martin, 1996, 1999).

We could determine the level of the survival index on the basis of the integral temperature regime (for four years). This level in the forecasting year determined by the water temperature allows us to identify the type of survival conditions and, consequently, the mean abundance of the year-class in this year.

At the next stage of the survival index estimation we should consider the qualitative and quantitative relationships between the survival index and the mean winter NAO index and the pressure gradient over the Barents Sea. The forecast of the mean winter NAO index and the pressure gradient in the given year could be made both with the dynamical models of the ocean-atmosphere system, e.g. the NCEP Forecast System, and with the array of statistical methods of climate forecasting (Rodionov and Martin, 1996, 1999).

As we have already noted, in years with the negative NAO mean winter indices, the survival indices of NEA cod are by 1.5-2 times higher. This could be considered an empirical rule for estimation of the survival indices and the year-class abundance.

The dynamical and statistical models for forecasting of pressure gradient over the Barents Sea help to specify the wind conditions during the spawning season as well as during the period of the cod larvae and juvenile growth.

Further, we consider the spawning stock biomass which, under the favorable conditions, should be low (~200,000 t) for appearance of strong year-classes. Under moderate survival conditions SSB should influence the recruitment abundance by 90%. Under unfavorable conditions, SSB determines the recruitment abundance by 37%. A more accurate assessment of the cannibalism role in regulation of the year-class abundance needs retrospective analysis of cod feeding in years with various biomass of the spawning stock.

This is a general scheme for forecasting of the year-class abundance both at the interannual and decadal time scales, based on the survival indices and three types of the survival conditions.

Relevance of the Ricker and Beverton-Holt models for determination of the generation abundance by the spawning stock

Bakun and Parrish recommended to apply the Beverton-Holt model (Bakun, Parrish, 1980) in case if the areas of the larvae dwelling and young cod feeding had a relatively constant ecological capacity. It is known that the Ricker equation has been applied widely for anadromous salmons, pelagic fish species, and benthic fish species, including cod (Ricker, 1954, 1958, 1963, 1975, Cushing, 1971, 1975, 1977, 1981, 1982, etc.).

Comparative studies made by the ICES WG (Anon., 1979) using observation data on the period of 1946-1975 revealed that the larger is the spawning stock the more abundant is the recruitment (Hylen, 2002). According to the Ricker model, the NEA cod recruitment maximum (6 mill. of fish at the age of 3) is produced by the spawning stock of 400,000 tons. However, application of the Beverton-Holt model to the same data showed that almost the same recruitment could be produce by a spawning stock varying in a very large range. Myers et al. (1995) made a compilation of extensive information about the fish species spawning stock and recruitment. Later the authors analyzed these data (Myers et al., 1996) and concluded that there was a somewhat general tendency of positive correlation between recruitment and the spawning stock biomass. This study as well as many others were based on application of the Ricker model to describe the recruitment - stock dependence for the NEA cod (Anon, 1979; Ricker, 1975; Garrod, Jones, 1974). However, scatter of values round the Ricker curve and also round the Beverton-Holt curve was too large to say anything definite (See Fig. 8 in Hylen, 2002). This cod population was studied by Garrod and Jones (1974) and Marshall et al. (1998). The latter concluded that the stock-recruitment problem could only be studied in the context of particular biological and environmental processes.

The NEA cod is characterized by great fluctuations in the year-class abundance. Sometimes, these fluctuations attain an order and a half of magnitude and repeat fairly regularly, similar to the types of conditions of the year-class abundance formation (Fig. 6). Dependence of recruitment on the spawning stock abundance, i.e. the stock density, estimated with a single-factor dispersion analysis was so low (Table 3) that there is no unambiguous answer to the question (Bondarenko et al., 2003).

We have computed abundance of year-classes with the Ricker and Beverton-Holt models in order to assess these prognostic tools. The least deviation of the generation abundance estimates from the observed values characterized the Ricker first formula (equation 3) (Table 5). Deviations varied from 397% to + 93%. The forecast abundance was only equal to the observed value in 1970. As to the Ricker second formula (equation 4), on the average, the deviation was twice larger than with the first formula, however, in percentage it was lower: from – 40% to + 97% (Table 5, Fig. 6).

The generation abundance estimates by the Beverton-Holt models also differed highly from the observed values. Minimum deviations were obtained with the 3rd method: from -151% to 85%, with the 4th method: from -313 to 75%, while the 2nd method yielded deviations from -672% to 58%.

The mean observed abundance of a year-class was 610 mln fish, while the result obtained with the 2nd method totaled 325 mln fish; the 3rd and the 4th methods showed 871 mln fish and 519 mln fish, respectively.

Such deviations of the estimates from the observed values indicate that the Ricker and Beverton-Holt models are not appropriate for quantitative expression of the recruitment – stock dependence and, consequently, for forecasting.

Conclusion

Clustering of the survival indices in the NEA cod year-class 3 allowed us to identify qualitative links and correlation between the spawning stock, the survival rates and the year-class abundance, temperature regime, and wind conditions, which exists under three types of the survival conditions: favorable, moderate and unfavorable.

It is shown that favorable conditions of survival (i.e. temperature and wind conditions) provide high survival rates and strong year-classes under one essential condition, i.e. a small spawning stock round 200,000 t. Obviously, this fact reveals a great role of cannibalism in the recruitment formation. Under favorable conditions of survival, the wind conditions are likely to affect survival more than the water temperature.

Under moderate conditions of survival (when the survival rates are average), the year-classes abundance depends on both the spawning stock, and the temperature and wind conditions.

Under unfavorable conditions of survival (low survival rates), there are large ranges between minimum and maximum values of all principal parameters: the spawning stock (1:10), the year-classes abundance (1:10), the water temperature and the NAO index. Almost 50% of generations appeared in cold and very cold years when the spawning stock was small. This explains the low abundance of year-classes. The wind conditions were also unfavorable for survival. Twenty years in the period of observations were characterized by the positive NAO mean winter indices. The negative NAO mean winter indices form a high gradient pressure zone over the Barents sea (Fig. 4). Large biomass of the spawning stock does not guarantee appearance of strong year-classes. Probability of their appearance is round 50%. However, these year-classes do not correspond to the spawning stock which is possibly associated with a high level of cannibalism.

Consideration of the three types of the survival conditions allowed us to determine the SSB critical level of 106,000 t (Bondarenko et al., 2003).

Great variations in dynamics of the recruitment reproduction under three types of the survival conditions suggests that it is necessary to forecast and consider survival conditions when developing the stock exploitation strategy, and moreover, the stock restoration plans.

It is also shown that the Ricker and Beverton-Holt models cannot any longer be considered efficient tools for determination of the recruitment-stock dependence in the NEA cod populations and provide necessary information for the fisheries management.

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Table 1. Spawning stock, year-class 3 abundance and survival index NEA cod (1946-2002)

Year	Spawning stock biomass(10^3 t)	Year-class 3 abundance (R), calculated with VPA (observed R, (*10^6)	Survival index (per 1t SSB) R/S	Survival index (per 10^6 eggs)
1	2	3	4	5
1946	1113	468	421	0.78
1947	1165	705	605	1.08
1948	1019	1084	1063	1.94
1949	730	1193	1635	3.06
1950	615	1590	2585	5.30
1951	569	642	1128	2.51
1952	521	273	524	1.31
1953	396	440	1109	2.85
1954	430	805	1873	5.16
1955	347	497	1432	3.73
1956	300	684	2280	6.15
1957	208	790	3799	10.72
1958	195	917	4693	13.73
1959	432	728	1684	4.81
1960	383	472	1231	3.83
1961	404	339	838	2.61
1962	312	777	2493	8.08
1963	208	1583	7601	24.87
1964	187	1295	6943	22.79
1965	102	165	1612	4.53
1966	121	112	928	2.66
1967	130	197	1519	4.24
1968	227	405	1781	5.83
1969	152	1015	6685	19.11
1970	224	1819	8103	25.28
1971	312	524	1681	5.30
1972	347	622	1794	5.85
1973	333	614	1844	6.45
1974	164	348	2116	6.65
1975	142	638	4496	14.43
1976	171	198	1159	3.74
1977	341	138	403	1.41
1978	242	151	625	2.07
1979	175	152	869	3.01
1980	108	167	1541	4.76
1981	167	398	2383	8.50
1982	326	524	1605	5.36
1983	327	1037	3168	12.22
1984	251	286	1140	4.49
1986	170	173	1015	4.74
1987	118	243	2052	4.33
1988	202	412	2038	7.42
1989	194	721	3711	6.72
1990	340	894	2631	10.85
1991	674	807	1198	7.26
1992	869	656	755	4.34

1	2	3	4	
1993	737	435	589	2.36
1994	601	714	1188	4.34
1995	499	840	1684	6.10
1996	571	584	1023	3.82
1997	564	641	1135	4.36
1998	386	498	1292	4.54
1999	253	498	1968	6.87
2000	221	681	3078	10.06
2001	322	308	958	3.62
2002	505	664	1315	4.80
N	57	57	57	57
Mean	374	610	2072	6.50
M.deviation	187	283	1180	3.68
St.deviation	249	379	1740	5.48
Max	1165	1819	8103	25.28
Min	102	112	403	0.78

Table 2. Role of spawning stock in formation of the year-class 3 abundance, 1946-2002

One way variance analysis

Groups, 10^3 t	***Counts***	***Sum***	***Mean***	***Dispersion***
SSB < 275	25	13092.70	523.71	221998.32
SSB 275 - 465	17	9468.58	556.98	47258.88
SSB 465 - 940	11	6802.45	618.40	169696.55
SSB >940	11	6802.45	618.40	169696.55

Source of variance	***SS***	***df***	***MS***	***F***	***P***	***F critical***
Between groups (Sz)	106461.57	3	35487.19	0.22	0.88	2.76
Inside groups (Sn)	9478032.83	60	157967.21			
Total (S)	9584494.39	63				

Role of SSB Ea=Sz/S=0.011, т.е. 1.1 %*

* - statistically insignifican*t*

Table 3. Role of survival factor (conditions) for abundance variance of year-class 3, 1946-2002

Cluster classification of survival conditions
One way variance analysis

Groups	*Counts*	*Sum*	*Mean*	*Dispersion*
Unfavourable	32	12768.16	399.01	69183.22
Moderate.	15	9166.03	611.07	101520.06
Favourable	9	9686.59	1076.29	165237.81

Source of variance	*SS*	*df*	*MS*	*F*	*P*	*F critical*
Between groups (Sz)	3266307.70	2	1633153.85	17.71	1.2 9	3.17
Inside groups (Sa)	4887863.05	53	92223.83			
Total (S)	8154170.74	55				

Role of factor Ea =Sz/S=401, т.е. 40.1%

Table 4. Reproductive parameters of NEA cod, 1946-2002

Population parameters	**Mean**	**Max**	**Min**
SSB (t •10^3)	373.95	1165.059	102.32
PF (eggs •10^{12})	132.99	651.32	32.71
3 year-class abundance (•10^6)	564.66	1818.950	112.04
Survival index (per 10^6 eggs)	6.18	25.28	0.78
Year-classess 3 classified by abundance (• 10^6)			
Strong	1269.49	1818.95	916.84
Average	594.21	804.78	439.60
Weak	242.74	408.09	112.04
Survival indices (per 10^6 eggs) of year classes of different strength			
Strong	14.12	25.28	1.94
Average	5.26	14.43	0.78
Weak	3.97	8.49	1.31
Survival conditions classified by the survival indices (per 10^6 eggs)			
Favourable	16.94	25.28	10.57
Moderate	6.40	8.49	5.16
Unfavourable	3.05	4.81	0.78

Table 5. Theoretical year-class 3 abundance cod (on Ricker's and observed and Beverton and Holt models and their generations (%) from observations-abundance

Year	Ricker's models					Beverton and Holt models						
	abundance (*10^6) calculated with formula 1	Deviation from obser-vations, %	abundance (*10^6) calculated with formula 2	Deviation from observation s,%	Method 1. a=1819, b - variable	abundance (*10^6), calculated with method 1	Deviation from obser-vations,%	Method 2. b=195, a - variable	abundance (*10^6), calculated with Method3 b=268, a =1819	Deviation from obser-vations %	abundance (10^6) calculated with Method 4	Deviations from obser-vations % Method 4
1	2	3	4	5	6	7	8	9	10	11	12	13
1946	171	-174	13780	97	3854	1195	61	550	1466	68	804	-49
1947	142	-397	15090	95	2302	1043	32	823	1479	52	812	-28
1948	238	-356	11645	91	627	776	-40	1291	1440	25	789	2
1949	619	-93	6507	82	-80	562	-112	1512	1330	10	725	22
1950	871	-83	4972	68	-887	386	-312	2094	1267	-26	688	44
1951	991	35	4415	85	971	684	6	862	1236	48	670	-2
1952	1125	76	3878	93	3199	1014	73	375	1201	77	650	-56
1953	1491	71	2654	83	1201	636	31	656	1085	59	584	-9
1954	1393	42	2961	73	166	450	-79	1170	1120	28	604	25
1955	1627	69	2226	78	773	514	3	776	1026	52	550	7
1956	1736	61	1848	63	114	342	-100	1128	960	29	513	33
1957	1814	56	1184	33	-311	188	-321	1531	795	1	421	55
1958	1803	49	1101	17	-529	150	-511	1832	767	-20	406	63
1959	1385	47	2987	76	352	488	-49	1057	1123	35	605	19
1960	1528	69	2539	81	1006	588	20	712	1071	56	575	-2
1961	1468	77	2725	88	1832	760	55	502	1094	69	588	-29
1962	1711	55	1941	60	-47	323	-141	1263	978	21	523	38
1963	1814	13	1186	-33	-1343	99	-1499	3065	795	-99	421	77

Continuation of Table 2

1	2	3	4	5	6	7	8	9	10	11	12	13
1964	1791	28	1043	-24	-1033	102	-1176	2649	747	-74	394	74
1965	1430	88	532	69	963	266	38	479	503	67	262	-1
1966	1555	93	638	82	1848	456	75	293	565	80	296	-54
1967	1605	88	691	71	1001	322	39	493	593	67	311	-3
1968	1819	78	1316	69	616	373	-9	752	835	52	443	16
1969	1702	40	824	-23	-743	93	-987	2319	658	-54	346	73
1970	1819	0	1297	-40	-1594	97	-1778	3399	829	-119	440	78
1971	1711	69	1940	73	558	441	-19	852	978	46	523	16
1972	1628	62	2223	72	392	435	-43	971	1026	39	550	21
1973	1662	63	2111	71	372	420	-46	974	1008	39	540	22
1974	1742	80	903	61	512	277	-26	761	692	50	365	24
1975	1663	62	764	16	-234	130	-391	1515	630	-1	331	61
1976	1760	89	945	79	1371	458	57	425	709	72	374	-22
1977	1642	92	2180	94	4371	1057	87	216	1019	86	546	-94
1978	1814	92	1416	89	2761	785	81	273	862	83	458	-71
1979	1768	91	967	84	1941	568	73	321	718	79	379	-50
1980	1474	89	566	71	1014	286	42	467	523	68	273	-5
1981	1749	77	918	57	366	252	-58	862	698	43	368	31
1982	1679	69	2056	75	610	464	-13	837	998	48	535	13
1983	1676	38	2064	50	-462	269	-285	1654	1000	-4	535	50
1984	1807	84	1484	81	1309	542	47	509	880	67	468	-16
1985	1800	89	1088	81	1515	516	60	411	763	73	403	-28
1986	1757	90	939	82	1620	504	66	371	707	76	373	-35
1987	1540	84	624	61	644	236	-3	643	557	56	291	19
1988	1810	77	1145	64	481	317	-30	809	782	47	414	23
1989	1801	60	1093	34	-231	185	-290	1444	764	6	404	54
1990	1645	46	2168	59	-203	319	-180	1407	1017	12	545	42
1991	735	-10	5724	86	712	680	-19	1040	1301	38	708	4
1992	396	-66	8733	92	1754	915	28	803	1390	53	760	-20
1993	606	28	6614	93	2651	1008	57	550	1334	67	727	-39
1994	907	21	4795	85	817	669	-7	946	1258	43	683	2
1995	1187	29	3649	77	240	507	-66	1169	1183	29	640	21

Continuation of Table 2

1	2	3	4	5	6	7	8	9	10	11	12	13
1996	985	41	4442	87	1194	727	20	784	1238	53	671	-8
1997	1003	36	4366	85	962	680	6	862	1233	48	669	-2
1998	1522	67	2559	81	910	570	13	750	1073	54	577	1
1999	1805	72	1497	67	427	360	-38	881	883	44	470	23
2000	1819	63	1275	47	-90	233	-192	1281	823	17	436	47
2001	1689	82	2019	85	1591	660	53	495	992	69	531	-24
2002	1170	43	3711	82	719	604	-10	920	1188	44	643	6
N	57	57	57	57	57	57	57	57	57	57	57	57
Mean	1432	34	2929	66	787	491	-104	1014	968	36	519	8
M.deviation	365	53	2052	22	852.14	210.63	221.28	475.3	215.38	30.4	121	30
St.deviation	467	94	3070	32	1165.22	267	371	663	258.24	43	145	38
Max	1819	93	15090	97	4371	1195	87	3399	1479	86	812	78
Min	142	-397	532	-40	-1594	93	-1778	216	503	-119	262	-94

Table 6. Favourable survival conditions classified by means of cluster analysis.

Year	SSB (10^3)	Year-class 3 abundance (•10^6)	Survival index (per 10^6 eggs)	The NAO mean winter index	T°C mean year (0-200 m) Kola sec.	T°C mean april (0-200 m) Kola sec.
1957	208	789.65	10.716	1.65	4.10	2.94
1958	195	916.84	13.733	-0.27	3.61	2.52
1963	208	1582.6	24.871	-0.97	3.40	2.20
1964	187	1295.4	22.793	-0.77	4.08	3.00
1969	152	1015.3	19.11	-2.09	3.68	2.40
1970	224	1818.9	25.281	-0.53	4.15	3.27
1975	142	638.49	14.429	1.16	4.38	3.56
1983	327	929.11	10.952	2.00	4.54	3.58
1989	194	700.26	10.568	2.86	4.47	3.12
N	9					
Mean	204	1076.3	16.939	0.50	4.04	2.95
St.deviation	53.126	406.5	6.157	1.638	0.402	0.494
Min	142	638.49	10.568	-2.09	3.40	2.20
Max	327	1818.9	25.281	2.86	4.54	3.58

Table. 7 Moderate survival conditions classified by means of cluster analysis

Year	SSB (10^3)	Year-class 3 abundance (•10^6)	Survival index (10^6 eggs)	The NAO mean winter index	T°C mean year (0-200 m) Kola sec.	T°C mean april (0-200 m) Kola sec.
1950	615	1590.377	5.301	1.20	4.73	3.86
1954	430	804.781	5.156	0.13	4.75	3.83
1956	300	683.69	6.153	-0.80	3.54	2.56
1962	312	776.941	8.082	-0.57	4.05	3.10
1968	227	404.774	5.828	-0.02	3.67	2.93
1971	312	523.916	5.299	-0.64	3.57	2.52
1972	347	621.616	5.848	0.08	4.05	2.85
1973	333	613.942	6.452	1.44	4.38	3.50
1974	164	348.054	6.653	0.49	4.01	2.87
1981	167	397.414	8.491	0.90	3.63	1.97
1982	326	523.102	5.352	0.25	3.66	2.56
1987	118	242.748	7.421	0.34	3.42	2.32
1988	202	408.093	6.679	0.10	3.75	2.85
1990	340	758.583	6.171	2.37	4.54	3.66
2000	221	468	7.036	1.85	4.67	3.79
N	15					
Mean	294	611.069	6.395	0.16	4.03	2.89
St.deviation	123.05	318.622	1.021	0.918	0.473	0.595
Min.	118	242.748	5.156	-0.80	3.42	1.97
Max.	615	1590.377	8.491	2.37	4.75	3.86

Table 8 . Unfavourable survival conditions classified by means of cluster analysis

Year	SSB (10^3)	Year-class 3 abundance (•10^6)	Survival index (per 10^6 eggs)	The NAO mean winter index	T°C mean year (0-200 m) Kola sec.	T°C mean april (0-200 m) Kola sec.
1946	1113	468.35	0.776	0.44	4.03	3.16
1947	1165	704.91	1.082	-1.07	4.25	3.43
1948	1019	1083.75	1.941	1.24	3.75	2.30
1949	730	1193.11	3.06	1.41	4.25	3.12
1951	569	641.58	2.508	-0.54	4.44	3.60
1952	521	272.78	1.307	0.62	4.17	3.04
1953	396	439.6	2.851	0.37	3.79	2.44
1955	347	496.82	3.733	-1.21	4.23	3.22
1959	432	728.34	4.807	0.36	4.37	3.30
1960	383	472.06	3.832	-0.15	4.34	3.50
1961	404	338.68	2.612	2.02	4.10	2.90
1965	102	164.96	4.529	-1.01	3.77	3.00
1966	121	112.04	2.658	0.23	2.83	1.60
1967	130	197.11	4.24	1.01	3.65	2.40
1976	171	198.49	3.745	0.59	4.11	3.10
1977	341	137.73	1.411	-1.10	3.55	3.02
1978	242	150.69	2.07	0.33	3.01	2.04
1979	175	151.82	3.014	-1.35	2.94	1.52
1980	108	166.79	4.757	0.07	3.60	2.70
1984	251	270.61	4.247	0.74	4.08	2.83
1985	193	202.9	4.696	-0.38	3.68	2.76
1986	170	172.79	4.334	-0.03	3.61	2.39
1991	674	516.2	2.781	0.21	4.49	3.55
1992	869	306.48	1.417	1.68	4.60	3.74
1993	737	252.29	1.372	1.43	4.07	3.32
1994	601	476.4	2.904	1.80	3.89	3.20
1995	499	579.16	4.217	2.44	4.35	3.44
1996	571	442.6	2.902	-2.32	3.76	2.80
1997	564	531.48	3.618	0.18	3.53	2.55
1998	386	454.66	4.142	0.80	3.63	2.44
1999	253	278	3.829	0.98	4.23	3.41
2001	322	165	2.091	-0.29	4.46	3.69
N	32					
Mean	435	399.01	3.046	0.08	3.92	2.86
St.deviation	292.565	263.03	1.199	1.078	0.450	0.567
Min	102	112.04	0.776	-2.32	2.83	1.52
Max	1165	1193.11	4.807	2.44	4.60	3.69

Table 9 . Role of SSB for abundance variance of year-class 3 under favorable conditions of survival in early life history, 1946-2002.

One way variance analysis

Groups, 10^3t	***Counts***	***Sum***	***Mean***	***Dispersion***		
SSB>170	2	1653.81	826.90	71000.05		
SSB 170-275	6	7103.68	1183.95	207063		
SSB<275	1	929.11	929.11			
Source of variance	***SS***	***df***	***MS***	***F***	***P***	***F critical***
Between groups (Sz)	215587.39	2	107793.69	0.58	0.59	5.14
Inside groups (Sa)	1106315.07	6	184385.85			
Total (S)	1321902.46	8				
Role of SSB Ea=Sz/S=0.163, т.е. 16.3%*						

* - statistically insignifican*t*

Table 10. Role of SSB for abundance variance of year-class 3 under moderate conditions of survival in early life history, 1946-2002

One way variance analysis

Groups, 10^3t	***Counts***	***Sum***	***Mean***	***Dispersion***		
SSB>260	6	2269.08	378.18	5857.80		
SSB 260-520	8	5306.57	663.32	12240.41		
SSB<520	1	1590.38	1590.38			
Source of variance	***SS***	***df***	***MS***	***F***	***P***	***F critical***
Between groups (Sz)	1306308.97	2	653154.50	68.17	2.80	3.89
Inside groups (Sa)	114971.91	12	9580.99			
Total (S)	1421280.87	14				

Role of SSB Ea=Sz/S=0.919, т.е. 91.9%

Table 11. Role of SSB for abundance variance of year-class 3 under unfavorable conditions of survival in early life history, 1946-2002.

One way variance analysis

Groups, 10^3t	***Counts***	***Sum***	***Mean***	***Dispersion***		
SSB>465	19	5299.08	278.89	27568.52		
SSB 465-940	10	5212.08	521.21	73084.71		
SSB>940	3	2257.01	752.34	96367.91		
Source of variance	***SS***	***df***	***MS***	***F***	***P***	***F critical***
Between groups (Sz)	797948.14	2	398974.07	8.59	0.001	3.33
Inside groups (Sa)	1346731.59	29	46439.02			
Total (S)	2144679.72	31				

Role of SSB Ea=Sz/S=0.372, т.е.37.2%

Table 12.Values of the NAO mean winter index in years of favorable and unfavorable conditions of the cod survival

Years	Survival index of cod	The NEO index (December-March)
Most favorable conditions		
1957 10	.72	1.52
1958 13	.73	-1.02
1963 24	.87	-3.60
1964 22	.79	-2.86
1969 19	.10	-1.20
1970 25	.28	-1.89
1975 14	.43	1.63
1983 10	.95	3.42
1989 10	.56	5.05
Least favorable conditions		
1977 1.	41	-2.14
1978 2.	07	0.17
1992 1.	42	3.28
1993 1.	37	2.67
2001 2.	09	-1.89

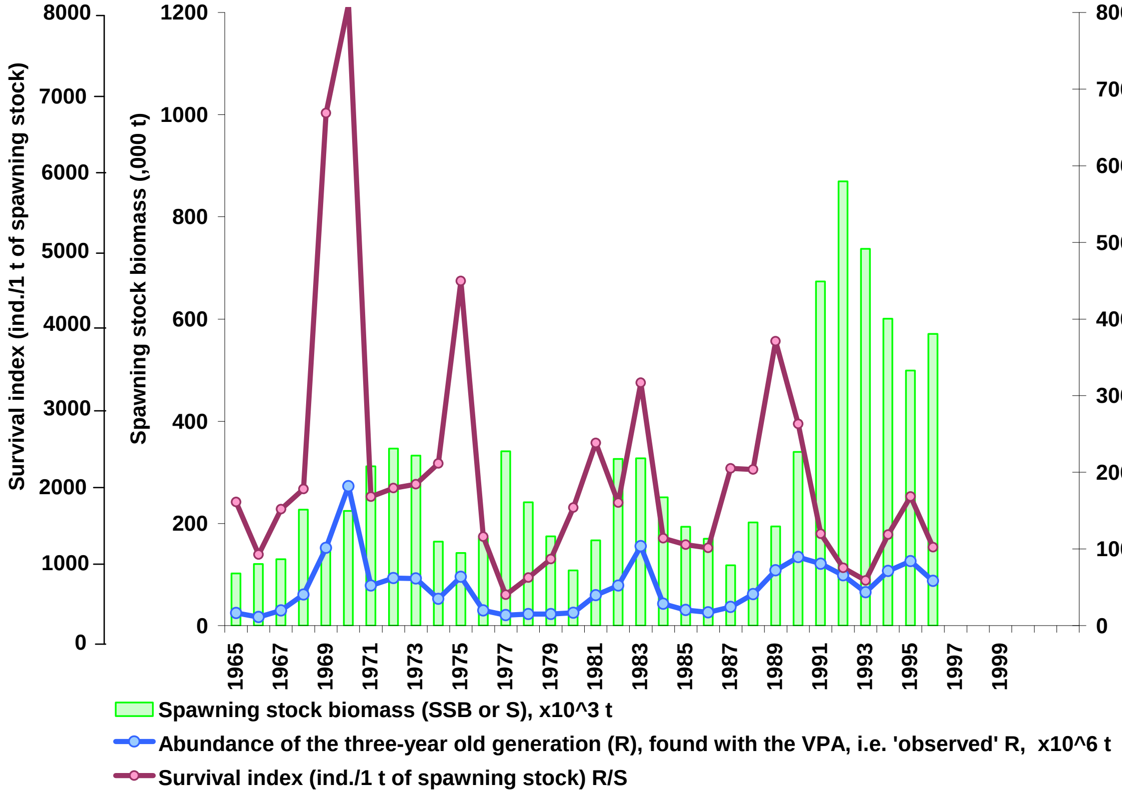

Fig. 1. Spawning stock, survival indice*s*, and year-class abundance of Northeast Arctic cod, 1946-1996.

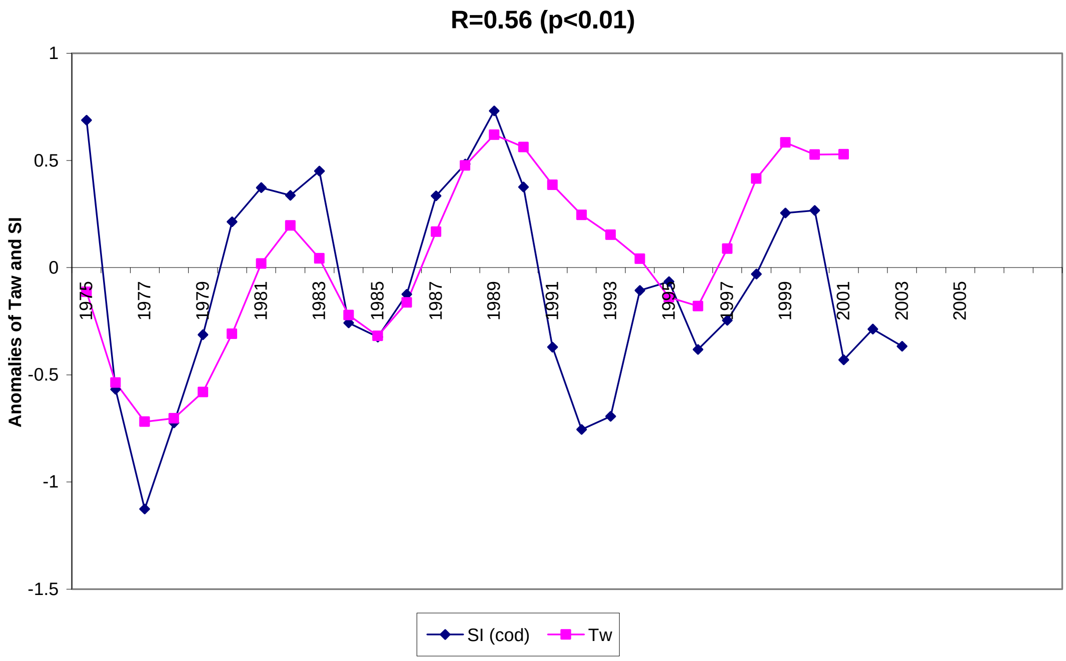

Fig. 2. Variations in integrated temperature anomalies* in the layer of 0-200 m (Kola section) and survival indice*s*, 1975-2001

* formula (2)

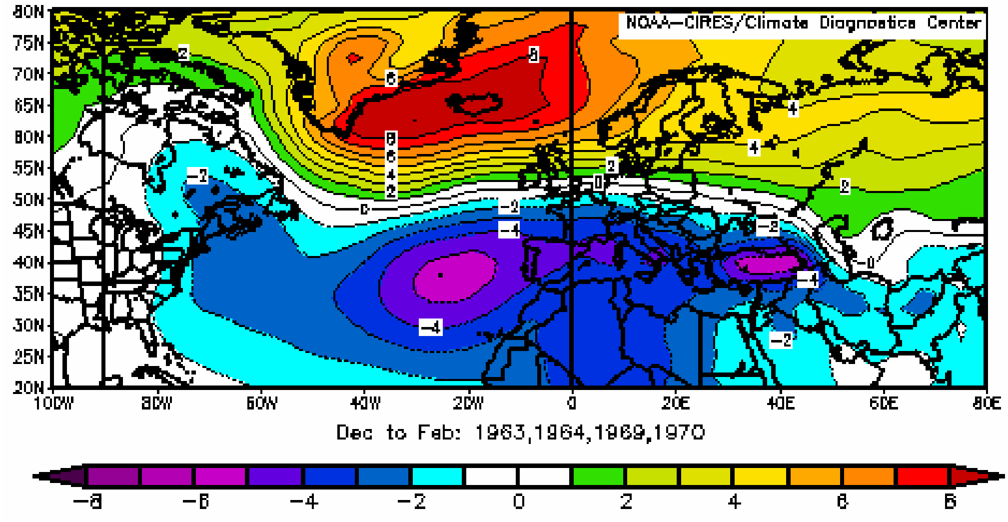

Fig.3 . Mean winter anomalies of sea level pressure in years most favorable for the NEA cod survival (1963, 1964, 1969, 1970).

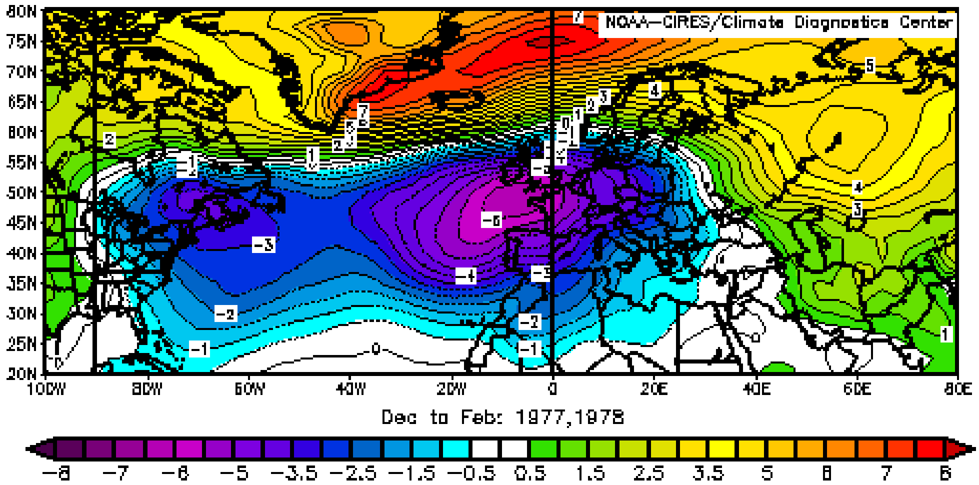

Fig. 4.. Mean winter anomalies of sea level pressure in years of least favorable conditions for the NEA cod survival under the negative NAO mean winter index (1977, 1978, 2001)

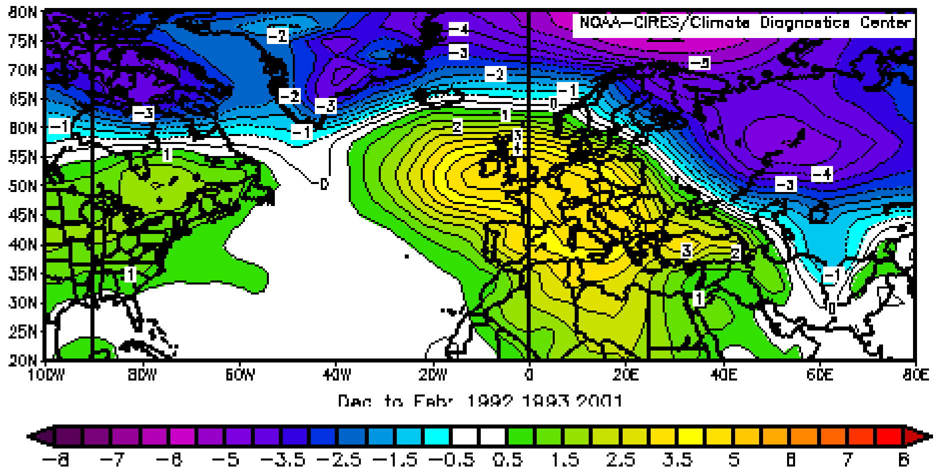

Fig. 5. Mean winter anomalies of sea level pressure in years of least favorable conditions for the NEA cod survival under

the positive NAO mean winter index (1992, 1993).

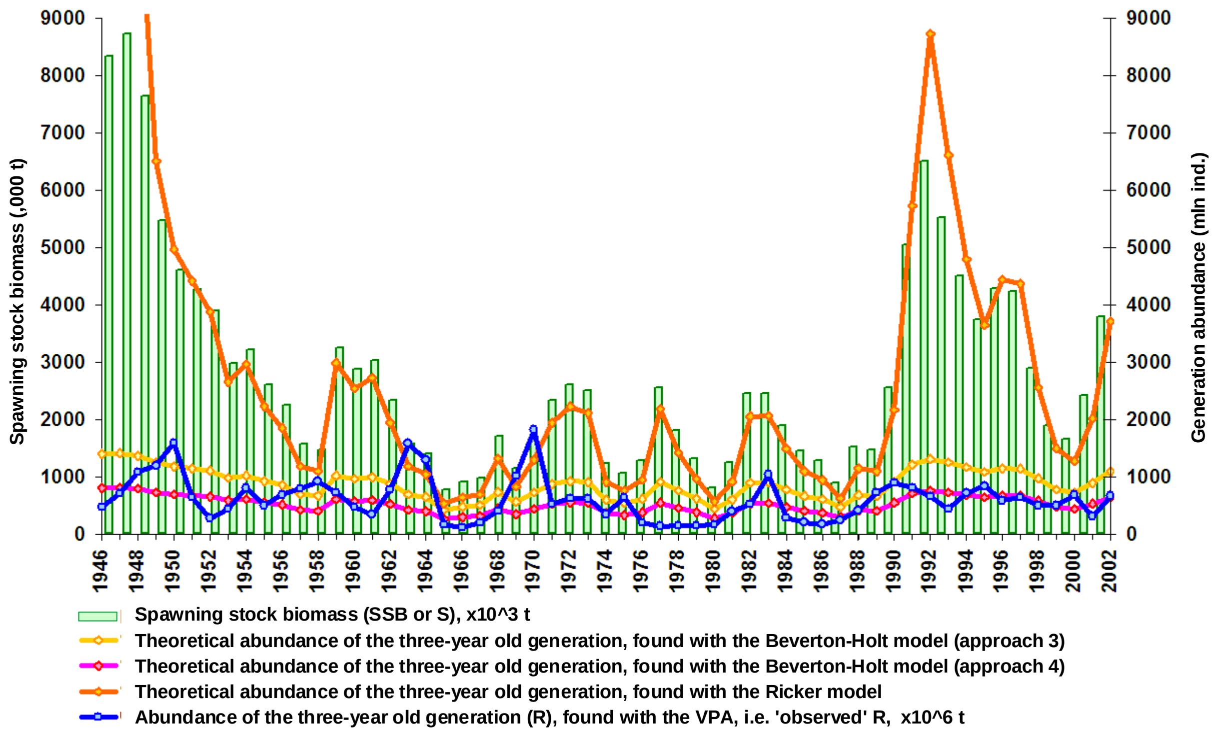

Fig. 6. Theoretical and observed year-class population abundance of Northeast Arctic cod, 1946-2002 .