

Predicting Year-class Strength Under Uncertainties Related to Survival in the Early Life History of Some North Atlantic Commercial Fish

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Abstract

Based on the nonparametric approach of the population fecundity concept, different levels of reproduction capacity were estimated in Norwegian spring-spawning herring, Barents Sea capelin, blue whiting, Northeast Arctic cod and Greenland halibut. Survival index of a year-class i.e. the ratio of the abundance of fish survived to age of recruitment to the total amount of eggs spawned taken equal to the population fecundity was used as an integrated indicator of ecological survival conditions during early life. Three different recurrent types of survival conditions during early life could be ranked out of the long time-series of the strength of year-classes and survival indices fluctuations. Those favourable, moderate and unfavourable conditions would stimulate to produce abundant, medium and poor year-classes correspondingly if the reproduction capacity of the population is not destroyed. Three levels of population fecundity needed to produce optimal recruitment under different types of survival conditions were calculated in the five populations of food fishes of the North Atlantic.

Introduction

The eventual abundance of a year-class at the very beginning of its life history is the total amount of eggs spawned by the maternal population. This could be measured in terms of population fecundity. Year-class survival during early life is the most important factor affecting the recruitment abundance. The rate of survival could be expressed as a ratio of a quantity of fish survived to age of recruitment to the total number of eggs spawned in a population during a particular spawning. Year-class survival rate can be regarded as an integrated index of survival conditions during early life. This index reflects biotic as well as abiotic factors of natural mortality during early life, either of which may be density independent or density dependent. Year-class survival index or something like it have been used before (Beverton, 1962; Beverton and Holt, 1957; Dragesund and Nakken, 1973; Nelson *et al.*, 1977; Schaaf, 1978; and others). An attempt was made in this paper not only to present long time-series of year-class survival rate fluctuations in comparison with reproduction capacity changes but also to assume probability of year-class abundance prediction based on the population fecundity concept. Most of the material presented has been published and the following are just some of them: Serebryakov *et al.* (1984), Serebryakov *et al.* (1985), Serebryakov *et al.* (MS 1989), Serebryakov (1990), Serebryakov *et al.*, (1990).

Materials and Methods

Year-class survival rate is found as per million of fish reaching maturity from the total amount of eggs laid during the spawning in the year of birth of this generation:

$$S_i = R_m \cdot 10^6 / E_{pi} \quad \dots (1)$$

where S_i — is the survival rate up to three-year-olds (or other age of first maturation) of the given generation (per million of eggs),

R_m — is the number of fish reaching maturity, and

E_{pi} — is the population fecundity in the given year.

The population fecundity is defined as the total sum of contributions of each age group to the overall amount of eggs which was shed by the population (Serebryakov, 1990).

There are three threshold levels defined of population fecundity "safe", "minimal required" and "critical". These can be identified as follows:

Safe Population Fecundity (SPF) is the level of population fecundity when the emergence of a strong

year-class is guaranteed under average survival conditions of the year-class as its early life history.

$$E_{\text{spf}} = R_{\text{ab}}/S_{\text{med}} \quad \dots (2)$$

Minimum Required Population Fecundity (MRPF) secures the appearance of strong year-classes under propitious survival conditions, medium year-classes in average and poor year-classes in unfavourable survival conditions.

$$E_{\text{mpf}} = R_{\text{av}} / S_{\text{med}} \quad \dots (3)$$

Critical Population Fecundity (CPF) provides for the appearance of strong year-classes only in the best survival conditions, but fails to ensure the delivery of generations of the average abundance under the average ecological conditions; a lower population fecundity would deprive the population of the opportunity to produce a strong year-class even in the best survival conditions.

$$E_{\text{cpf}} = R_{\text{ab}} / S_{\text{max}} \quad \dots (4)$$

where E_{spf} — is the safe population fecundity,

E_{mpf} — is the minimum population fecundity,

E_{cpf} — is critical population fecundity,

R_{ab} — is the lowest defined abundance of a strong year-class at age of recruitment,

R_{av} — is the lowest defined abundance of a medium year-class at age of recruitment,

S_{med} — is the observed average survival rate of a medium year-class during early life, and

S_{max} — is the maximum survival rate during early life for the period of observations.

Abundance of fish aged 3 years (R_{III}) was used as the criterion for herring, capelin, cod and blue whiting year-class strength and age 5 (R_{V}) for Greenland halibut as indicated in the table below:

Year-class category	Herring ($R_{\text{III}} \times 10^9$)	Capelin ($R_{\text{III}} \times 10^{11}$)	Cod ($R_{\text{III}} \times 10^9$)	Blue whiting ($R_{\text{III}} \times 10^9$)	G. halibut ($R_{\text{V}} \times 10^7$)
Strong	>7.0	>3.5	>1.0	>1.0	>6.5
Medium	2.0-7.0	2.5-3.5	0.5-1.0	0.5-1.0	5.1-6.5
Poor	<2.0	<2.5	<0.5	<0.5	<0.0

Results

Norwegian spring-spawning herring (Fig. 1). Year-class abundance fluctuations in this herring are exceptionally great. For example, the strong year-class of 1959 at age 3 exceeded the poor year-class of 1956 by

125 to 1 even though the population fecundities in the year of birth of these year-classes were nearly equal. The year-class strength variation range made up over three orders of magnitude: $2,117.5 \times 10^6$ of 3-year-olds in 1959 and 6×10^6 in 1971. Strong year-classes would appear both in years of exceptionally high population fecundity, e.g. in 1951, and in relatively low years, e.g. in 1963. Poor year-classes come about both during high population fecundity years, as was the case in 1955, and in low years as was observed annually since 1965. The emergence of generations of medium abundance follows a similar pattern.

Year-class survival rate until age 3 varied quite significantly through the period of studies, in fact by nearly three orders of magnitude. The maximum survival rate was in 1973, the minimum was in 1968. Those year-classes turned out to be poor in both cases. The 1968 year-class turned out to be a poor one due to low survival, but the 1973 year-class was due to low fecundity.

The period of 33 years covered by research witnessed a change in the population fecundity of spring-spawning Atlantic herring by over two orders of magnitude. The maximum population fecundity was observed in 1955 ($1,446.1 \times 10^{12}$ eggs), the minimum was in 1972 (4.7×10^{12} eggs). The level of population fecundity generally went down after 1958 while it had decreased by over two orders of magnitude between 1965 and 1972.

The overexploitation of strong year-classes in the 1960s coupled with the unfavourable survival conditions observed in 1965-68 made the spawning population of herring in the early 1970s consist of individuals from poor year-classes. The population fecundity was very low: two to three orders of magnitude less than the level observed in the 1950s and early 1960s. Even under the best survival conditions the emergence of a strong year-class was theoretically improbable, given such a population fecundity. To attain that, one has to have a population fecundity of at least 175×10^{12} .

In 1983 the population fecundity of herring ran up to 81.4×10^{12} , i.e. slightly above one-half CPF which made possible a strong year-class under the best survival conditions.

Capelin of the Barents Sea (Fig. 2). The population fecundity of capelin between 1972 and 1986 varied from 31.8×10^{14} to 1.8×10^{14} eggs. Strong year-classes were recorded both in years of exceptionally high population fecundity in 1976, and when it was close to the average in 1972. Survival rates for these year-classes turned out to be 116 and 287 per million of eggs respectively.

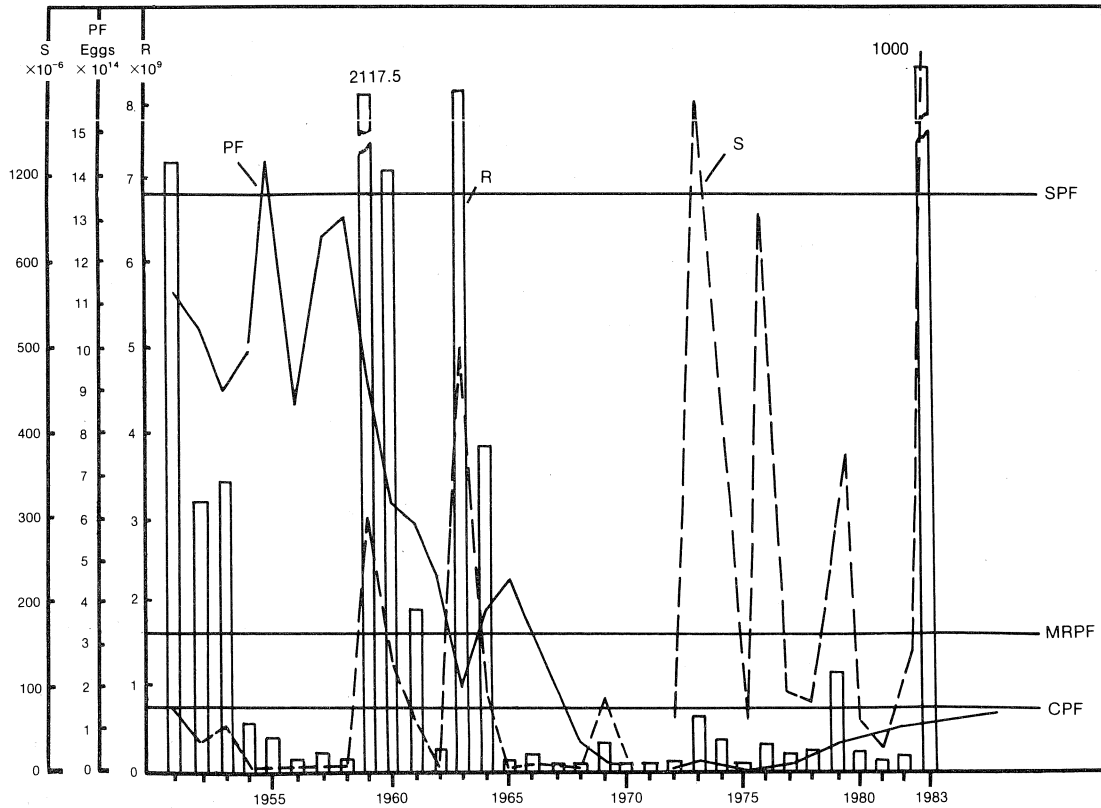


Fig. 1. Norwegian spring-spawning herring population fecundity (PF), year-class strength (R) and survival index (S).

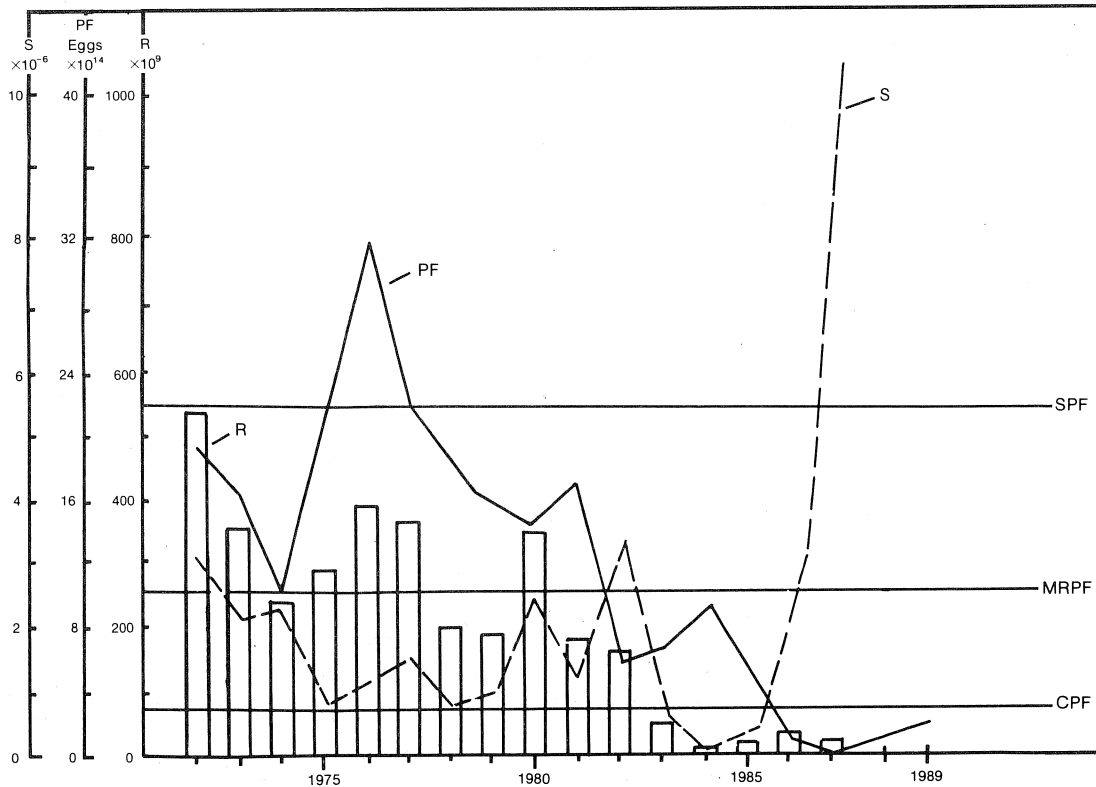


Fig. 2. Barents Sea capelin population fecundity (PF), the year-class strength (R), and survival index (S).

The strong 1972 year-class had a better survival than in 1978 by about three times whereas their population fecundity was nearly equal. Conversely, in the case of nearly equal survival observed in 1976, 1977, 1979 and 1981 there appeared generations of various strength: average in 1977, strong in 1976, poor in 1979 and 1981.

Northeast Arctic cod (Fig. 3). This fish had a maximum population fecundity in 1947 (3.8×10^{14} eggs), minimum in 1980 (0.3×10^{14} eggs); variations in population fecundity exceeding one order of magnitude. The number of 3-year-olds throughout the period studied varied between 0.09×10^9 and 2.5×10^9 . Survival variations are over one order of magnitude: from 23.5 per million of eggs for the strong year-class of 1964 to 1.2 per million of eggs for the poor year-class of 1946.

Strong year-classes appear both in years of exceptionally high population fecundity (e.g. 1948) and in years when this value was low (e.g. 1964). Poor year-classes, like strong ones, appear both in years of exceptionally high population fecundity (e.g. 1946) and very low years (e.g. 1979).

The average rates of survival to age 3 of strong, medium and poor year-classes were 14, 9 and 4 per million of eggs respectively. Given a nearly equal population fecundity, the survival rate in a strong year-class (e.g. 1964) is greater than that of a poor year-class (e.g.

1966) by more than an order of magnitude.

Survival conditions facilitating the appearance of a strong year-class were set up for eight times throughout the period of study. It was only for four cases that they were taken advantage of: 1963, 1964, 1969 and 1970; the remainder of cases consisted solely of generations of medium strength.

The conditions when only poor year-classes could be expected were observed for 12 times during the period of study but only 10 year-classes of that period happened to be poor, while 1 year-class was strong (1948) and the other medium (1947). The population fecundity in the two latter instances was exceptionally high.

In 1982 the population fecundity of Arctic cod reached 83.2×10^{12} eggs at the expense of the bulk of the 1975 year-class being recruited into the spawning population. This exceeded MRPF, and made the appearance of a strong year-class possible should the ecological conditions at early stages be favourable in 1983. The potential created by the level of population fecundity was realized when an abundant year-class developed under favourable survival conditions.

Blue whiting (Fig. 4). The blue whiting year-class strength fluctuations were not so significant within the period of 1970–85 as they were with the herring or cod.

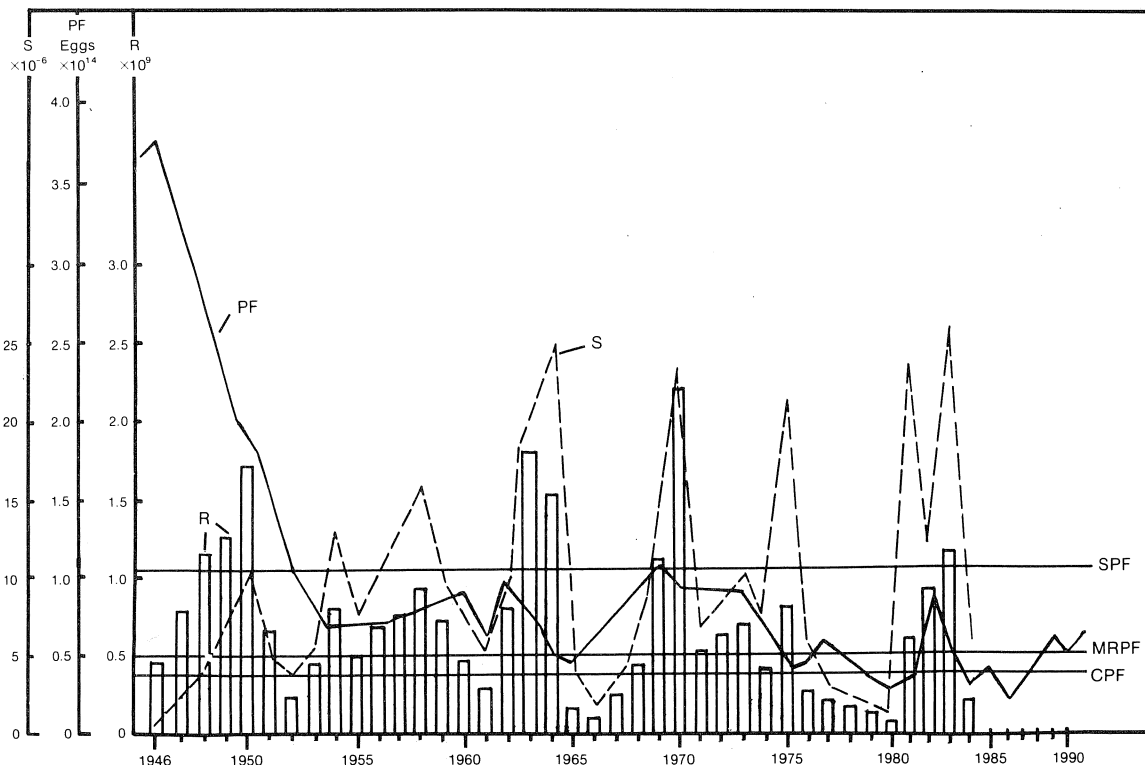


Fig. 3. Arctic cod population fecundity (PF), year-class strength (R) and survival index (S).

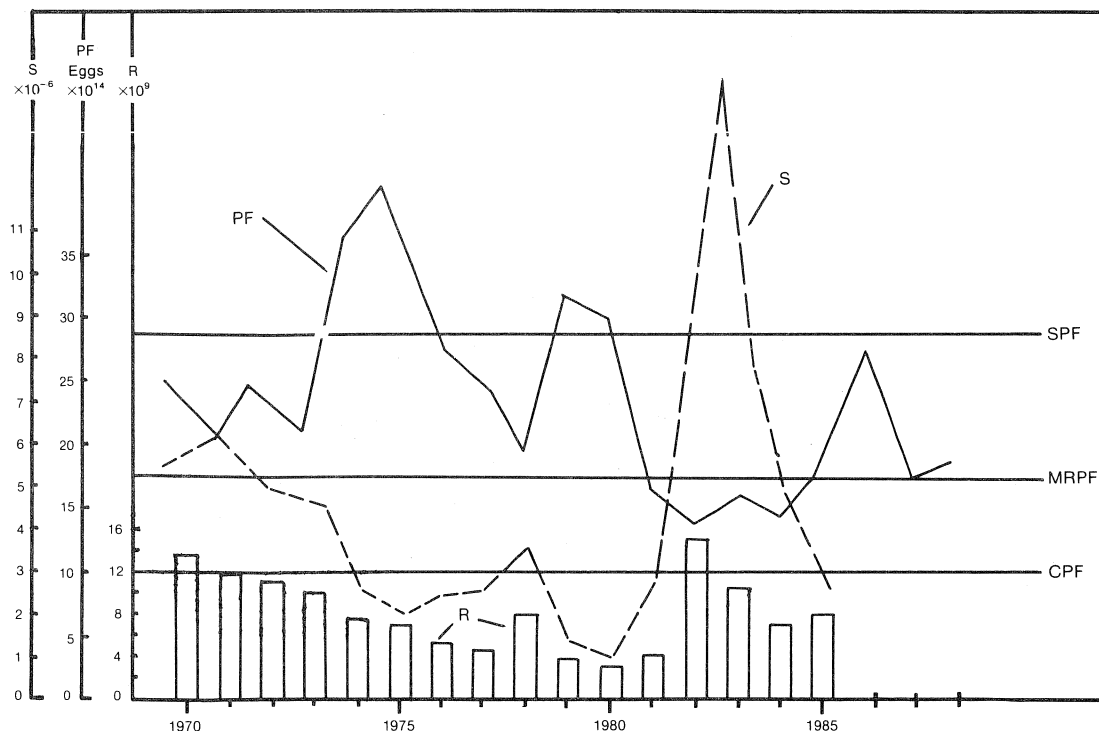


Fig. 4. Blue whiting population fecundity (PF), year-class strength (R) and survival index (S).

The richest blue whiting 1982 year-class exceeded the poorest one of 1980 by a factor of 4.7. The changes of population fecundity have been not great either. The maximal population fecundity of 1975 was higher than the minimal one of 1982 by 2.5 times. Survival index fluctuations were significantly greater reaching one order of magnitude: from 1.1 in 1980 to 11.0 in 1982 per million of eggs.

Greenland halibut (Fig. 5). Significant variations were found in population fecundity and abundance of 5-year olds in the Greenland-Canadian population. The population fecundity varied from 844.2×10^9 eggs in 1969 to $2,446.6 \times 10^9$ in 1976. Survival rate coefficients as estimated in the year-classes of 1969–83 showed more significant fluctuations than the population fecundity. There was a five-fold difference between the maximum (1982) and minimum (1977) survival rates.

Discussion

Year-class abundance fluctuations were greatest in Norwegian spring-spawning herring. They exceeded two orders of magnitude even before the drastic drop in population fecundity, i.e. prior to 1967. The strong 1970 year-class of Northeast Arctic cod exceeded the abundance of the poor 1980 year-class by 60 times. The smallest fluctuations of year-class abundance were

seen in capelin; only about one order of magnitude (Fig. 1–5).

Strong year-classes of all the species investigated appeared both in years of exceptionally high population fecundity, and years when this characteristic was relatively low. The same was true of the emergence of generations of poor and medium abundance. A mere collation of the strength of a year-class with population fecundity did not reveal a close relationship between the recruitment and population fecundity. This was due to the well known fact that the formation of year-class abundance depends heavily on the survival conditions at the early life history, i.e. throughout the embryonic, larval and fingerling periods of life.

The most insignificant survival rate was in the case of Norwegian spring-spawning herring of the 1967 year-class 0.17×10^{-6} . The greatest fluctuations of this parameter by nearly 2.5 orders of magnitude made up another feature of this population. In comparison the survival rate in Barents Sea capelin was within the range of only 287 to 65 per million eggs.

During the period of 1967–82 the cause for low abundance (i.e. poor level) of all generations of the herring could be found in the low amount of eggs spawned rather than in the unfavourable surrounding ecological conditions for survival at the early stages of life history. Judging by the survival factor during this

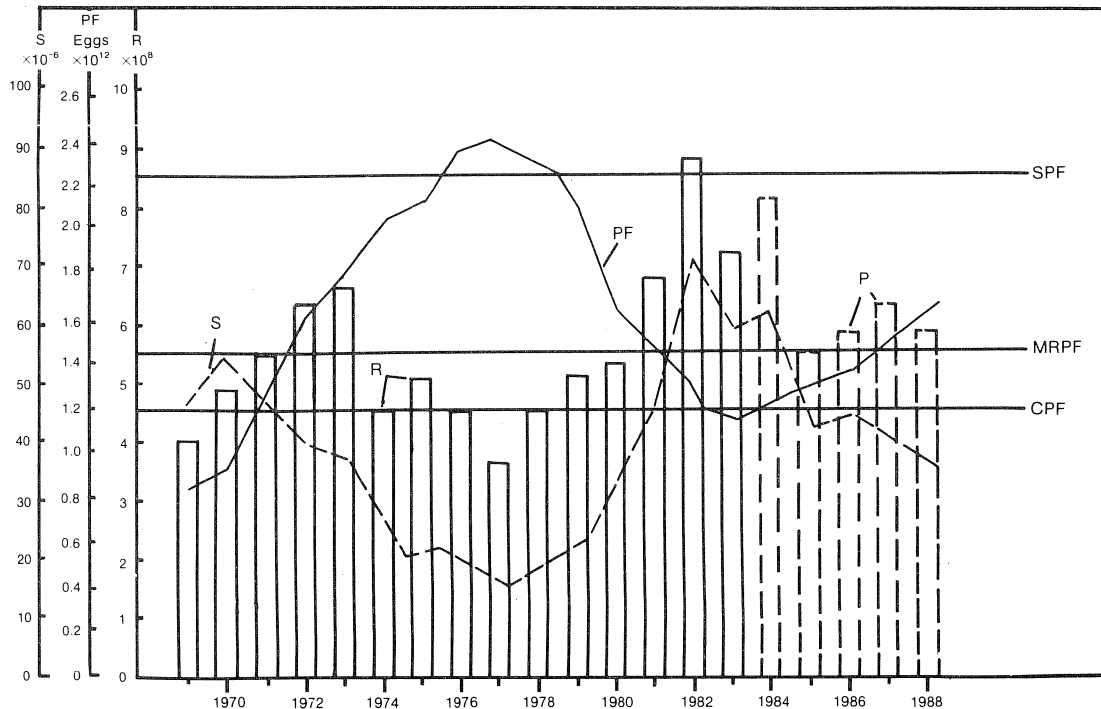


Fig. 5. Greenland halibut population fecundity (PF), year-class strength (R), survival index (S) and projected year-class strength.

period, there even could have appeared strong year-classes, specifically in 1973, 1974, 1976 and 1979, had the population fecundity been sufficiently high (Fig. 1).

Survival rate assessment is one of the possible ways to analyze the dynamics of fish abundance. This parameter can be used to narrow the possible field of search for the factors which lead to the appearance of poor year-classes. Thus we have to seek the causes for low abundance caused by low survival at the early stages only in the years when there were low survival rates rather than in each year when generations were scarce.

Determination of levels of spawning stock which represent different levels of reproduction capacity is another aspect of the application of retrospective analysis of population fecundity, year-class strength and survival rates.

Population fecundity of Norwegian spring-spawning herring reached levels of "critical population fecundity" (CPF) in 1966-67, Northeast Arctic cod in 1979-81, Barents Sea capelin in 1985-87, Greenland halibut in 1969-70, and it has not reached CPF in the case of blue whiting yet (Fig. 1 to 5). The high intensity of fishing for herring continued after reaching CPF which resulted in decreasing the population fecundity to such a low level that it entailed a series of poor year-classes even under propitious survival conditions

at the early stages of development, and a consequent deep long-term depression in stock abundance. It was only in 1983 that the population fecundity had reached the level of approximately one half of CPF which made a potential for the emergence of an abundant year-class, in the event of the very best survival conditions.

The blue whiting reproduction capacity is influenced by the same features as the Atlanto-Scandian herring one. These are (a) low individual fecundity, which give the age composition an important role, (b) long life cycle of mature fish. For the sake of preventing a catastrophe with the blue whiting stock, its population reproduction capacity must be kept and preserved at the level of minimal required population fecundity. Allowable catch should be established considering the estimation spawning stock biomass which could safely ensure MRPF.

In 1983, Northeast Arctic cod population fecundity rose above the level of CPF which provided for the appearance of a year-class of strong abundance under good survival conditions at the early stages of life.

Greenland halibut population fecundity of the critical level was observed in 1969 and 1970, when the poor year-classes emerged under moderate survival index. In all the other cases, the Greenland halibut population fecundity was either close or well above the critical level.

TABLE 1. Three levels of herring, capelin and cod population fecundity (eggs $\times 10^{12}$).

Species	Safe population fecundity	Medium required population fecundity	Critical population fecundity
Norwegian spring-spawning herring	1,346	570	175
Barents Sea capelin	2,500	1,045	300
Arctic cod	128	64	42.5
Blue whiting	2,759	1,739	978
Greenland halibut	2.3	1.5	1.2

Given a particular population fecundity, different year-class strengths could be predicted under uncertainties related to survival in early life history as alternatives depending on survival conditions, if we have the critical population fecundity so that the only case when abundant year-class could be theoretically expected is maximal favourable survival conditions during early life. The "natural" year-class abundance fluctuations in dependence of survival conditions could be expected when "minimal" required population fecundity is given, and one can theoretically expect abundant year-class development from "safe" population fecundity even under moderate survival conditions. These different "expectations" could be regarded as different risk levels in management when particular spawning stocks are considered. Depending on the strategy of utilization of some fish population, and on the fisheries management objectives, the basic parameter for the determination of the projected spawning stock size in each specific case may be chosen from one of the three levels of population fecundity: SPF, MRPF or CPF (Table 1). The most cautious treatment here must be given to the exploitation of the population on the CPF level.

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