Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations

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Abstract

A long-term (1907–98) virtual population analysis (VPA) was made for Norwegian spring-spawning herring (NSSH), which is a huge pelagic fish stock in the north-east Atlantic. It shows that this herring stock has had large fluctuations during the last century; these fluctuations have mainly been determined by variations in the temperature of the inflowing water masses to the region. The spawning stock biomass (SSB) increased from a rather low level in the early years of this century and reached a high level of around 14 million tons by 1930. The spawning stock biomass then decreased to a level of around 10 million tons by 1940, but increased again to a record high level of 16 million tons by 1945. The stock then started to decrease and during the next 20-year period fell to a level of less than 50 000 tons by the late 1960s. Through the 1970s and 1980s, the stock slowly recovered and after the recruitment of strong year classes in 1983 and 1990–1992 the stock recovered to a spawning stock biomass of about 10 million tons. The long-term fluctuation in spawning stock biomass is caused by variations in the survival of recruits. It is found that the long-term changes in spawning stock abundance are highly correlated with the long-term variations in the mean annual temperature of the inflowing Atlantic water masses (through the Kola section) into the north-east Atlantic region. The recruitment is positively correlated with the average temperature in the Kola section in the winter months, January–April, which indicates that environmental factors govern the large-scale fluctuations in production for this herring stock.

Keywords herring and climate, herring biomass fluctuations, temperature, time series

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Introduction

Marine fish populations vary in abundance. This has been known long before it became a science to study fish abundances in the early years of this century. This fact causes challenges both for scientists and for fishery managers throughout the world. One of the first scientists to take note of the variations in fish abundance in the north-east Atlantic was Johan Hjort (1914) who described the variation in abundance of a few important fish stocks. Since then, it has been an everlasting challenge for scientists to find the answer to what governs the great changes in abundance. Is it varying food supply for the youngest life stages which influences the survival of the fry or is it variations in the abundance of predators? Does the direct influence of physical parameters, such as temperature or salinity, have any effect? These questions and many more have been studied throughout the last century in an attempt to shed light on the central question: why do fish stocks vary in abundance? In this context, long time series of data are particularly valuable. Bits and pieces of the answer fall into place now and then for different stocks, and the relation between physical oceanographic factors and biological parameters has been shown for a few stocks (Myers 1998; Ottersen *et al.* 1998; Michalsen *et al.* 1998).

The Norwegian spring-spawning herring (NSSH) is a stock which has undergone large fluctuations. There were times when the herring were abundant, enriching the environment and the people who harvested it along the coast of Norway, while in other periods the herring were more or less absent (Devold 1963; Sejerstad 1986; Try 1986; Fladby 1987; Dyrvik 1988; Mykland 1988; Nedkvitne 1988). In the beginning of the 20th century, Norwegian fishery investigations were organized and sampling of catches from the most important commercial fish stocks were started in 1907. Every year since then, systematic sampling of the NSSH catch has been carried out.

The Norwegian spring-spawning herring is one of the stocks in the so called Atlanto-Scandian group of herring stocks (Johansen 1919). There are three stocks in this group and the other two are the spring-spawners at Iceland and the summer-spawners in the same area. The three stocks have certain similarities: they dwell in high latitudes (around Iceland and in the Norwegian Sea); they grow to a fairly large maximum size of about 40 cm; and the two spring-spawners have shown the ability to migrate over large distances (Devold 1963).

The Norwegian spring-spawners spawn in early spring (February–March) off the Norwegian coast in an area ranging from approximately 59°00′ N to about 69°00′ N (Devold 1963) (Fig. 1). The most important spawning grounds are found close to the coast between 62°00′ N and 63°00′ N. The larvae drift northwards with the Norwegian coastal current and end up in the Barents Sea or in the fjords in northern Norway (Dragesund 1970). By the end of summer (which is short at these

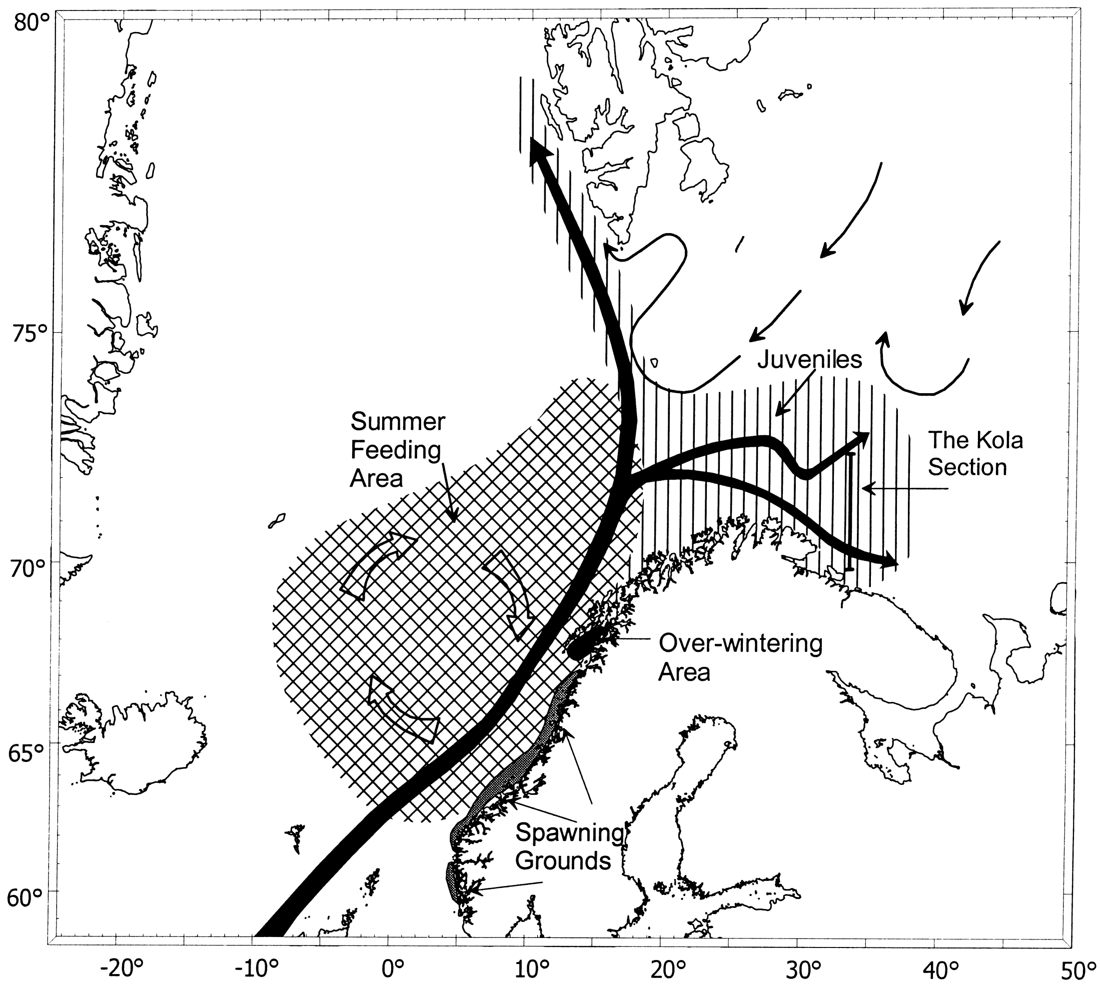

Figure 1 Distribution area of Norwegian spring-spawning herring in the north-east Atlantic region. Open arrows = migration route of herring during summer; thick arrows = main flow of Atlantic water; thin arrows = main flow of cold Arctic water.

latitudes), in July, the larvae metamorphose and start shoaling. They stay in the nursery region until spring in their third year of life and then migrate southwards along the Norwegian coast where they mix with older age-groups. At the age of 5–8 years (depending on growth), they mature to spawn (ICES 1999).

After spawning, the adult stock migrate, from the Norwegian coast, in a north-westerly direction, into the Norwegian Sea (Devold 1963). Here they feed during the summer from May to September. The stock then migrates back to the Norwegian coast where it aggregates close to shore, in a small region in northern Norway. Here the spawning stock and young pre-spawning age-groups over-winter in dense concentrations. In January, the stock starts to migrate southwards along the Norwegian coast, where they spawn when they are ripe.

The study of the long-term changes in abundance of fish stocks and the identification of factors behind those changes may form a basis for enhanced management in the future. Fisheries are generally known to play a major role in the dynamics and changes in fish stocks. This is mainly because fish stock assessment is a relatively new science that has developed after the expansion of the modern fishery industry. If we could study the fluctuations in a fish stock before this expansion–in the so called virgin state of the stock–and point at environmental factors which were correlated to these fluctuations, we might extract useful information about the controlling factors behind the production in fish stocks. Such information may enable us to better manage these stocks. The very long time series of data needed for such studies are scarce, and to conduct an analytical assessment of a fish stock certain data are needed: (i) reliable fishery statistics and (ii) representative sampling of biological data from the fisheries (including age determination). Both these elements were fulfilled for the NSSH from the very start of sampling in the early 1900s, and it is therefore possible to carry out a long-term analytical assessment of this stock. The first virtual population analysis (VPA) was made for the NSSH stock by Dragesund and Ulltang (1978), and covered the years back to 1950. Since then, VPAs have been carried out annually to describe analytically the historical development of the stock. Recently, data on the age distribution in the period prior to 1950 was compiled for all years back to 1907 and contains information on the age distribution of the stock for the different fisheries. A long-term VPA ranging from 1907 to 1998 is presented in this paper.

Long-term analyses of stock abundances and the study of the relation between these and environmental time series may shed light on the basic question; why do fish stocks vary in abundance? Several authors (Ellertsen *et al.* 1984; Ellertsen *et al.* 1987; Sætersdal and Loeng 1987; Ellertsen *et al.* 1989; Bjørke and Sætre 1994; Sundby 1994; Loeng *et al.* 1995; Ottersen 1996; Helle and Pennington 1999; Planque and Frédou 1999) have studied the environmental impact on recruitment variability, larval growth and the distribution of Arcto-Norwegian cod (*Gadus morhua*, Gadidae). This stock spawns in the same environment as the NSSH stock and it may be assumed that the environmental factors that impact recruitment of the cod stock also affect the recruitment of herring.

In the present paper, we aim both to describe the nearly one hundred years of fluctuations in abundance of a fish population in the northern boreal regions, and to illustrate that the large-scale fluctuations in stock abundance may be caused by natural environmental factors and not by the activities of fisheries. The relationship between water temperature (an oceanic climatic index), spawning stock biomass (SSB) and recruitment for Norwegian spring-spawning herring is studied and we pose the following two questions:

1 Is there a significant relationship between long-term fluctuations in spawning stock size for the Norwegian spring-spawning herring and long-term fluctuations of the temperature of the inflowing Atlantic water-masses to the north-east Atlantic region?

2 Is there any relationship between the recruitment to the stock and the temperature in the water-masses where the young stages of the herring live?

Methods and materials

Long-term virtual population analysis

Fishery data

The data used in the long-term VPA are fishery statistics for the different fisheries for NSSH and weight at age data needed for converting the catch in tons to numbers per year class for each year. We used data from a VPA of the stock for the period 1950–97 produced by ICES (1999). The biological data for earlier years (before 1950) and how they are derived and used are described below:

Input data for the population analysis are in Tables 1–5.

Catch data

The catch data (Table 1 and Fig. 2) for different periods are as follows: for the years 1950–98, catch statistics for the NSSH as reported to ICES (ICES 1999); for the years 1918–50 catch statistics as compiled by an international group of scientists in 1995 which dealt with the zonal distribution of the stock (Report of the scientific working group on zonal attachment of Norwegian spring spawning herring 1995), and finally for the period 1907–17, data from the *Bulletin Statistique des Pêches Maritimes*, which were the official catch statistics as reported from each country to the International Council for the Exploration of the Sea (*Bulletin Statistique des Pêches Maritimes des Pays du Nord de l'Europe* 1910–1912, 1914, 1917, 1919, 1922).

Biological sampling and catch in numbers at age

The conversion of catch in weight to catch in number at age is based on annual biological samples from catches in the different fisheries. The number of fish aged during the winter/spring season annually in the years 1907–50 is shown in Table 2.

The fisheries for NSSH may be divided into four main groups: (i) the small herring fisheries, targeting 0- and 1-year-olds in the Norwegian fjords and off northern Norway; (ii) the fat herring fisheries, targeting 2- and 3-year-olds off the coast of northern Norway; (iii) the winter herring fisheries, targeting adult mature herring during the spawning season; and (iv) the herring fisheries off Iceland in summer and early autumn. This division of the fishery represents the traditional herring fishery and it applies to the period before the breakdown of the stock in the late 1960s. The fishery statistics for the years before 1950 are based on this division. After 1977, fisheries

Table 1 Landings of Norwegian spring-spawning herring 1907–98 (× 1000 tonnes).

Year	Total landings	Fat herring	Small herring	Adult off Iceland	Adult Norway	Year	Total landings	Fat herring	Small herring	Adult off Iceland	Adult Norway
1907	207.6	50.1	20.9	19.3	117.3	1953	1074.4	79.8	160.9	155.1	678.6
1908	233.4	61.6	34.3	21.9	115.6	1954	1644.5	130.0	208.1	187.3	1119.1
1909	288.5	114.0	40.0	18.8	115.6	1955	1359.8	39.7	103.1	213.1	1003.9
1910	250.0	89.4	29.6	15.3	115.7	1956	1659.4	103.7	95.1	267.8	1192.8
1911	253.5	61.2	70.1	6.2	116.0	1957	1318.5	40.6	129.6	291.8	856.5
1912	245.2	44.6	74.0	10.7	116.0	1958	986.3	55.2	146.1	355.9	429.1
1913	290.7	27.8	50.3	18.7	193.9	1959	1111.1	48.1	179.9	372.9	510.2
1914	356.0	37.6	101.4	23.0	193.9	1960	1101.8	48.7	232.0	420.1	401.0
1915	306.1	41.8	44.8	25.6	193.9	1961	830.1	88.5	243.7	351.6	146.3
1916	296.9	28.4	48.4	26.1	194.0	1962	848.6	161.2	136.2	417.7	133.5
1917	276.2	31.2	41.1	10.0	193.9	1963	984.5	140.9	172.8	538.0	132.8
1918	433.5	52.5	64.6	8.2	308.2	1964	1281.8	57.2	106.7	697.7	420.2
1919	498.1	47.4	110.8	19.1	320.8	1965	1547.7	105.1	117.0	934.6	391.0
1920	316.5	38.8	49.1	16.7	211.9	1966	1955.0	152.9	78.5	1091.7	631.9
1921	258.5	35.4	71.1	17.0	135.0	1967	1677.2	438.6	107.0	672.7	458.9
1922	349.9	78.7	49.7	37.7	183.7	1968	712.2	412.8	26.3	227.8	45.3
1923	330.5	26.3	34.0	9.2	261.0	1969	67.8	29.3	14.4	–	24.1
1924	295.0	14.8	55.6	8.3	216.3	1970	62.3	3.9	37.5	–	20.9
1925	355.5	17.0	42.4	16.4	279.7	1971	21.1	13.1	1.1	–	6.9
1926	403.8	16.7	103.8	28.6	254.7	1972	13.2	–	–	–	13.2
1927	489.9	25.3	110.9	71.9	281.8	1973	7.0	–	–	–	7.0
1928	611.9	124.8	117.3	69.3	300.6	1974	7.6	–	–	–	7.6
1929	624.6	84.1	133.8	63.2	343.5	1975	13.7	–	–	–	13.7
1930	704.5	41.8	111.6	76.2	475.0	1976	10.4	–	–	–	10.4
1931	538.2	12.9	117.5	100.2	307.7	1977	22.7	–	–	–	22.7
1932	652.6	41.3	155.1	91.4	364.8	1978	19.8	–	–	–	19.8
1933	818.2	178.5	219.0	90.8	329.9	1979	12.9	–	–	–	12.9
1934	451.7	112.9	132.6	95.2	111.0	1980	18.6	–	–	–	18.6
1935	649.4	36.5	138.4	73.8	400.8	1981	13.7	–	–	–	13.7
1936	775.2	31.0	112.9	150.0	481.4	1982	16.7	–	–	–	16.7
1937	695.9	18.5	123.9	237.0	316.4	1983	23.1	–	–	–	23.1
1938	783.6	9.4	121.2	156.8	496.3	1984	53.5	–	–	–	53.5
1939	703.4	25.8	122.8	148.7	406.2	1985	169.9	–	–	2.6	167.3
1940	923.1	44.3	277.6	204.2	397.0	1986	225.3	–	–	26.0	199.3
1941	594.0	71.5	217.0	95.2	210.3	1987	127.3	–	–	18.9	108.4
1942	592.7	51.8	145.5	145.0	250.4	1988	135.3	–	–	20.2	115.1
1943	556.6	47.8	106.4	177.0	225.4	1989	103.8	–	–	15.1	88.7
1944	587.8	13.3	69.4	216.4	288.7	1990	86.4	–	–	11.8	74.6
1945	554.4	29.3	124.3	60.0	340.8	1991	84.7	–	–	11.0	73.7
1946	586.2	28.2	64.6	150.1	343.2	1992	104.4	–	–	13.3	91.1
1947	710.4	20.3	47.1	195.8	447.2	1993	232.5	–	–	32.7	199.8
1948	1012.6	17.9	87.8	86.1	820.7	1994	479.2	–	–	98.4	380.8
1949	783.0	21.8	101.1	94.6	565.5	1995	905.5	–	–	375.7	529.8
1950	826.1	29.7	72.9	54.8	668.7	1996	1220.3	–	–	521.2	699.1
1951	1277.8	75.0	208.6	104.9	889.3	1997	1426.5	–	–	565.5	861.0
1952	1254.8	33.2	302.4	89.8	829.4	1998	1223.1	–	–	479.2	743.9

(i) and (ii) no longer existed because a minimum size regulation of 25 cm was applied. After 1994, fishery (iv) was developed with participation from several European countries, and is currently a summer fishery in the feeding area in the Norwegian Sea (Fig. 1). The following procedure was followed in order to convert the catch in tons to catch in numbers per age group:

The catch of small herring (0- and 1-year-olds) was divided between the two age groups on the basis of their relative strength as 9- and 10-year-olds. The catch of the two age groups was then converted to numbers by using the mean weights of 0- and 1-year-olds for the period 1950–65 (ICES 1999). Likewise, the catch of fat herring (2- and

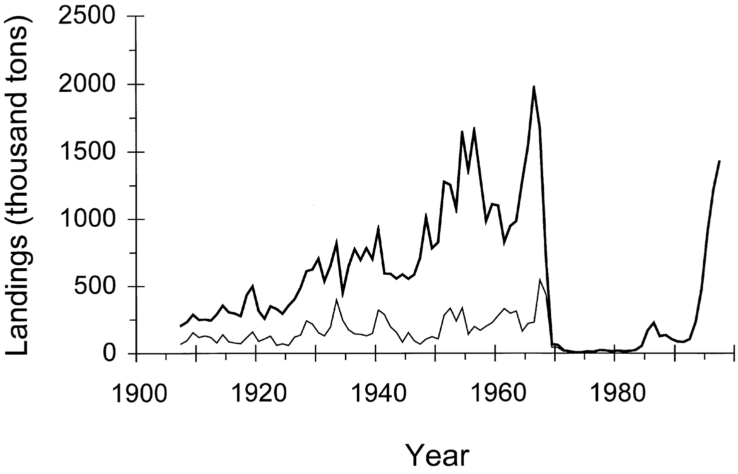

Figure 2 Landings of Norwegian spring-spawning herring, 1907–1997. Thick line = total landings; thin line = landings of young herring.

3-year-olds) was divided between the two age groups on the basis of their relative strength as 9- and 10-year-olds. The catch of these two groups was then converted from weight to numbers by dividing the mean weight for the 2- and 3-year-olds in the period 1950–65 (ICES 1999).

The catch of adults in winter/spring is split according to the observed age distribution in samples from the fishery on the spawning grounds in each year from 1907 to 1950. The number of fish aged is in Table 2. The mean weight per age group in the catch (ICES 1999) for the mature age groups during the years 1950–65 was used to convert the catch in tons to catch in numbers. For the years 1935–41, data on mean weight at age in the catches were available, and were used for these years. The weights at age are in Table 3.

The catch of adults in summer/autumn on Icelandic grounds and in the Norwegian Sea was split according to the observed age distribution in samples from the herring fishery in Iceland each year from 1930 to 1968.

The catch in numbers at age are in Table 4. The remaining input data for a VPA–natural mortality at age, maturation at age and weight at age–are presented in Table 5.

Calculation of stock size

The starting point for the part of the VPA covering the period 1907–50 was the stock numbers at age in 1950 as estimated by ICES (1999). The number of fish at age 10 (which was chosen as a reference age) was calculated for this age group on the basis of the catch in numbers at this age per year applying the following equation:

$$N_t = \frac{C_t}{(1 - e^{-Z_t})}\left(\frac{F_t + M}{F_t}\right)$$

where C_t is the catch during the year t and F and M are estimated or assumed values of fishing mortality and natural mortality.

The age group 10 was chosen as a reference age because this is the age at which the relative strength of the cohort is representative because the herring was fully recruited to the spawning stock by the age of 10 years (ICES 1999). The F at the reference age for the years 1907–28 was derived from Lea (1930). Lea estimated an overall average survival rate of 0.81 for adult NSSH. However, in his paper, the survival rate is given as a mean proportion surviving each year. Recalculating to instantaneous rates, the total mortality is 0.21, and assuming a natural mortality equal to the level in recent years of 0.15, the average fishing mortality of adult herring is estimated to be 0.06 for the period 1907–28. A fishing mortality of 0.0375 for reference age (10-year-olds) in the years 1929–49, is taken from the estimated fishing mortality at this age for the years 1950 and 1951 (ICES 1999). In these years, the SSB was estimated by ICES (1999) at more than 12 million tons, and it is assumed that this level of fishing mortality applies to this age group (10-year-olds) for the period in which the stock probably was at its highest abundance.

From this starting point, the stock size (number of fish at age) was derived by applying Pope's approximation for calculating N_t (Pope 1972; Hillborn and Walters 1992):

Table 2 Number of fish aged in Norwegian and Icelandic adult fisheries 1907–50.

Year	Norway	Iceland	Year	Norway	Iceland
1907	924	–	1929	4951	–
1908	1498	–	1930	5101	–
1909	1258	–	1931	5841	–
1910	1066	–	1932	6402	–
1911	1849	–	1933	7111	–
1912	1089	–	1934	5347	–
1913	316	–	1935	7287	–
1914	3255	–	1936	7388	–
1915	4227	–	1937	6944	–
1916	9284	–	1938	5563	–
1917	6396	–	1939	5955	2399
1918	1931	–	1940	6095	2385
1919	6178	–	1941	4041	1970
1920	4372	–	1942	3823	1169
1921	6373	–	1943	2476	2671
1922	3289	–	1944	3114	448
1923	4684	–	1945	4671	418
1924	4718	–	1946	4845	2013
1925	8083	–	1947	4700	1611
1926	7684	–	1948	2726	1907
1927	5173	–	1949	4090	569
1928	6028	–	1950	6114	1269

$$N_t = N_{t+1}e^{M} + C_t e^{\frac{M}{2}}$$

where N_t is number in the year t, M is natural mortality and C_t is catch in the year t. Fishing mortality was calculated as:

$$F = -\ln\left(\frac{N_t}{N_0}\right) - M.$$

Pope's approximation assumes that all the catch takes place in the middle of the year.

In reality, this is not the case. Fishing occurs during various periods and often more or less continuously throughout the year. However, it is shown that if total mortality (Z) is small, the approximation is good (Hillborn & Walters 1992) and even if Z is large, the discrepancy between the method based on the assumption of continuous fishing and the approximation is less than 10%.

The number of fish in the cohort as 9-year-olds was calculated based on the catch of 9-year-olds and adjusting positively for the natural mortality. The number of fish as 11-year-olds was, on the other hand, calculated from the number of 10-year-olds by withdrawing the catch as 10-year-olds and adjusting negatively for natural mortality.

Calculation of spawning stock biomass

The SSB was calculated as the product of the number at age, the proportion mature at that age and the weight at age. The resulting biomass for each age-group is then summed over the entire range of ages.

The proportion mature at age is a function of the growth rate of the cohort. Because observations on maturation at age are sparse for the years prior to 1950, the average proportion of maturation for each age group for the years 1950–65 was used for the period 1907–49.

The weight at age for the period prior to 1950 was calculated in the same way as the proportion mature for each age group. For some years (1935–41 and 1948), data were available on weight at age in the spawning stock and these observed weights were used for the years in which they were observed.

Stock size and recruitment in relation to climate

The water temperature in the Kola section (see Fig. 1) is an indication of the temperature regime in the water masses where the herring live their first 6 months. Data from this section has been used in earlier studies of environmental impact on recruitment in fish stocks in the north-east Atlantic, and it comprises a long time series of data (Ottersen 1996). The annual average for 0–200 m from 1900 to 1997 (Bochkov 1982) were used. Data from recent years have been provided by PINRO, Murmansk, Russia. The average values for the months January–April for the years 1921–94 were provided by the Institute of Marine Research, Bergen, Norway.

The annual values were smoothed using the moving average:

$$Sm(x_t) = \frac{1}{2q+1}\sum_{r=-q}^{+q} x_{t+r}.$$

Two smoothed series of the temperatures in the Kola section were made. One series smoothed over 19 years ($q = 9$) and the other of the average temperature in winter (January–April) smoothed over 5 years ($q = 2$). The first series was related to the long-term fluctuations in SSB, while the winter temperature series (smoothed and unsmoothed) was related to recruitment as 0-group fish. The number of 0-group fish is likely to be better correlated to the temperature than the number of fish as 3-year-olds because they have been influenced by various environmental factors for a longer time.

Table 3 Weight in stock (kg).

Age	1907–34	1935	1936	1937	1938	1939	1940–47	1941	1942	1948–54	1949	1950	1955	1956	1957	1958	1959	1960	1961
0	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
1	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008
2	0.047	0.060	0.060	0.047	0.050	0.060	0.047	0.047	0.047	0.047	0.047	0.047	0.047	0.047	0.047	0.047	0.047	0.047	0.047
3	0.100	0.129	0.123	0.116	0.087	0.098	0.100	0.060	0.100	0.119	0.100	0.100	0.100	0.100	0.100	0.100	0.100	0.100	0.100
4	0.199	0.180	0.157	0.173	0.162	0.172	0.186	0.102	0.199	0.194	0.199	0.204	0.195	0.205	0.136	0.204	0.204	0.204	0.232
5	0.237	0.185	0.201	0.191	0.185	0.205	0.206	0.197	0.237	0.223	0.237	0.230	0.213	0.230	0.228	0.242	0.252	0.270	0.250
6	0.267	0.247	0.229	0.229	0.216	0.218	0.212	0.217	0.267	0.278	0.267	0.255	0.260	0.249	0.255	0.292	0.260	0.291	0.292
7	0.286	0.273	0.270	0.246	0.253	0.239	0.249	0.234	0.286	0.297	0.286	0.275	0.275	0.275	0.262	0.295	0.290	0.293	0.302
8	0.307	0.284	0.298	0.282	0.266	0.264	0.264	0.270	0.307	0.305	0.307	0.290	0.290	0.290	0.290	0.293	0.300	0.321	0.304
9	0.315	0.305	0.307	0.294	0.288	0.276	0.284	0.281	0.315	0.304	0.315	0.305	0.305	0.305	0.305	0.305	0.305	0.318	0.323
10	0.324	0.306	0.318	0.314	0.307	0.292	0.291	0.295	0.324	0.312	0.324	0.315	0.315	0.315	0.315	0.315	0.315	0.320	0.322
11	0.332	0.303	0.326	0.312	0.308	0.311	0.314	0.302	0.332	0.316	0.332	0.325	0.325	0.325	0.325	0.330	0.325	0.344	0.321
12	0.339	0.309	0.320	0.319	0.316	0.300	0.317	0.304	0.339	0.326	0.339	0.330	0.330	0.330	0.330	0.340	0.330	0.349	0.344
13	0.348	0.310	0.325	0.316	0.317	0.311	0.324	0.324	0.348	0.331	0.348	0.340	0.340	0.340	0.340	0.345	0.340	0.370	0.357
14	0.354	0.309	0.330	0.322	0.314	0.309	0.321	0.321	0.354	0.333	0.354	0.345	0.345	0.345	0.345	0.352	0.345	0.379	0.363
15	0.368	0.321	0.335	0.321	0.319	0.308	0.318	0.321	0.368	0.349	0.368	0.362	0.362	0.362	0.362	0.360	0.355	0.375	0.365

Age	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
0	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
1	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.015	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.010
2	0.047	0.047	0.047	0.047	0.047	0.047	0.047	0.047	0.047	0.080	0.070	0.085	0.085	0.085	0.085	0.085	0.085	0.085	0.085
3	0.100	0.100	0.100	0.100	0.100	0.100	0.100	0.100	0.100	0.100	0.150	0.170	0.170	0.181	0.181	0.181	0.180	0.178	0.175
4	0.219	0.185	0.194	0.186	0.185	0.180	0.115	0.115	0.209	0.190	0.150	0.259	0.259	0.259	0.259	0.259	0.294	0.232	0.283
5	0.291	0.253	0.213	0.199	0.219	0.228	0.206	0.145	0.272	0.225	0.140	0.342	0.342	0.342	0.342	0.343	0.326	0.359	0.347
6	0.300	0.294	0.264	0.236	0.222	0.269	0.266	0.270	0.230	0.250	0.210	0.384	0.384	0.384	0.384	0.384	0.371	0.385	0.402
7	0.316	0.312	0.317	0.260	0.249	0.270	0.275	0.300	0.295	0.275	0.240	0.409	0.409	0.409	0.409	0.409	0.409	0.420	0.421
8	0.324	0.329	0.363	0.363	0.306	0.294	0.274	0.306	0.317	0.290	0.270	0.404	0.444	0.444	0.444	0.444	0.461	0.444	0.465
9	0.326	0.327	0.353	0.350	0.354	0.324	0.285	0.308	0.323	0.310	0.300	0.461	0.461	0.461	0.461	0.461	0.476	0.505	0.465
10	0.335	0.334	0.349	0.370	0.377	0.420	0.350	0.318	0.325	0.325	0.325	0.520	0.520	0.520	0.520	0.520	0.520	0.520	0.520
11	0.338	0.341	0.354	0.360	0.391	0.430	0.325	0.340	0.329	0.335	0.335	0.534	0.543	0.543	0.543	0.543	0.543	0.551	0.534
12	0.334	0.349	0.357	0.378	0.379	0.366	0.363	0.368	0.380	0.345	0.345	0.500	0.482	0.482	0.482	0.482	0.500	0.500	0.500
13	0.347	0.341	0.359	0.387	0.378	0.368	0.408	0.360	0.370	0.355	0.355	0.500	0.482	0.482	0.482	0.482	0.500	0.500	0.500
14	0.354	0.358	0.365	0.390	0.361	0.433	0.388	0.393	0.380	0.365	0.365	0.500	0.482	0.482	0.482	0.482	0.500	0.500	0.500
15	0.358	0.375	0.402	0.394	0.383	0.414	0.378	0.397	0.391	0.390	0.390	0.500	0.482	0.482	0.482	0.482	0.500	0.500	0.500

Table 3 *(cont.)*

Age	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
0	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
1	0.010	0.010	0.010	0.010	0.010	0.010	0.010	0.015	0.015	0.008	0.011	0.007	0.008	0.010	0.018	0.018	0.018	0.018
2	0.085	0.085	0.085	0.085	0.023	0.085	0.055	0.050	0.100	0.048	0.037	0.030	0.025	0.025	0.025	0.025	0.025	0.025
3	0.170	0.170	0.155	0.140	0.148	0.054	0.090	0.098	0.154	0.219	0.147	0.128	0.081	0.075	0.066	0.076	0.096	0.074
4	0.224	0.204	0.249	0.204	0.234	0.206	0.143	0.135	0.175	0.198	0.210	0.224	0.201	0.151	0.138	0.118	0.118	0.147
5	0.336	0.303	0.304	0.295	0.265	0.265	0.241	0.197	0.209	0.258	0.244	0.296	0.265	0.254	0.230	0.188	0.174	0.174
6	0.378	0.355	0.368	0.338	0.312	0.289	0.279	0.277	0.252	0.288	0.300	0.327	0.323	0.318	0.296	0.261	0.229	0.217
7	0.387	0.383	0.404	0.376	0.346	0.339	0.299	0.315	0.305	0.309	0.324	0.355	0.354	0.371	0.346	0.316	0.286	0.242
8	0.408	0.395	0.424	0.395	0.370	0.368	0.316	0.339	0.367	0.428	0.336	0.345	0.358	0.347	0.388	0.346	0.323	0.278
9	0.397	0.413	0.437	0.407	0.395	0.391	0.342	0.343	0.377	0.370	0.343	0.367	0.381	0.412	0.363	0.374	0.370	0.304
10	0.520	0.453	0.436	0.413	0.397	0.382	0.343	0.359	0.359	0.403	0.382	0.341	0.369	0.382	0.409	0.390	0.378	0.310
11	0.543	0.468	0.493	0.422	0.428	0.388	0.362	0.365	0.395	0.387	0.366	0.361	0.396	0.407	0.414	0.390	0.386	0.359
12	0.512	0.506	0.495	0.437	0.428	0.395	0.376	0.376	0.396	0.440	0.425	0.430	0.393	0.410	0.422	0.384	0.360	0.340
13	0.512	0.506	0.495	0.437	0.428	0.395	0.376	0.376	0.396	0.440	0.425	0.470	0.374	0.410	0.410	0.398	0.393	0.344
14	0.512	0.506	0.495	0.437	0.428	0.395	0.376	0.376	0.396	0.440	0.425	0.470	0.403	0.410	0.410	0.398	0.391	0.385
15	0.512	0.506	0.495	0.437	0.428	0.395	0.376	0.376	0.396	0.440	0.425	0.470	0.400	0.410	0.405	0.398	0.391	0.363

Results

The VPA estimates are in Tables 6–8 and Figs 3–7.

Development of the spawning stock biomass

As shown in Fig. 3, the SSB increased from a rather low level of 2 million tons in 1907 to a level of about 5 million tons in 1911. This increase was due to the rather rich 1904 year class (see Fig. 4) which entered the spawning stock fully during 1911 and 1912. In the following years, the stock decreased to about 2 million tons in 1920. It then increased again due to good recruitment, first the 1913 year class, and later more abundant year classes, such as 1918, 1922, 1923 and 1925. The stock reached a high level in 1930 with a SSB of about 14 million tons. The stock then decreased to around 9 million tons in 1939, but increased rapidly during the early 1940s to a record high of 16 million tons in 1945. This increase was caused by several abundant year classes in the 1930s (Fig. 4). After 1946, the spawning stock decreased almost continuously until the stock collapsed in the late 1960s. The decrease was interrupted briefly due to recruitment of the rich 1950 and 1959 year classes. In the period 1970–75, the SSB was estimated to be less than 100 000 tons. During the 1970s and early 1980s, the stock increased very slowly and then accelerated due to the recruitment of the 1983 year class in the late 1980s. In the late 1990s, the spawning stock increased further because of the recruitment of the rich 1991 and 1992 year classes. Poor recruitment after 1993 has caused a decrease in SSB from 1998 onwards (ICES 1999).

Effect of the fishery and fishing mortality

The landings of Norwegian spring-spawning herring throughout the period 1907–98 are given in Fig. 2 and in Table 1. By the turn of the 19th century, the total landings were about 200 000 tons, but soon increased to a level of about 250 000–300 000 tons. The total quantity increased somewhat during the first 25 years of the century, to a level of about 400 000 tons by 1926. During the following five years, the total landings increased to a level of about 700 000 tons. This level was held until late 1940s. Throughout the first 60 years of the century, the estimated instantaneous fishing mortality coefficient (F; Cushing 1968; Fig. 5, mean for age groups 5–12 years) was less than 0.15. The landings increased but so did the spawning stock biomass. During the 1950s,

Table 4 Catch at age (millions).

Age	1907	1908	1909	1910	1911	1912	1913	1914	1915	1916	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929
0	644	1335	1455	1748	2262	4033	3070	2254	1917	2933	1914	3799	3952	1963	2552	2897	1719	1404	2203	2108	2279	7992	2243
1	950	1281	1600	514	3092	1613	768	5489	1500	760	1225	1130	4505	1787	2877	900	877	2840	1029	5814	6185	959	7974
2	108	206	523	518	331	391	134	305	380	94	199	474	329	340	188	468	140	128	128	63	196	377	257
3	461	494	773	498	364	115	182	122	95	229	156	123	210	101	214	426	158	40	65	127	91	1041	698
4	154	86	3	66	2	4	8	14	6	67	166	14	51	29	8	86	34	25	28	15	186	82	163
5	129	52	210	43	14	10	19	22	57	50	121	222	57	38	90	161	405	67	52	160	124	334	155
6	103	59	58	255	84	19	31	37	28	105	25	123	355	28	16	115	129	321	72	49	81	158	313
7	88	62	22	32	261	68	14	28	33	27	49	35	134	205	19	9	94	116	380	69	50	82	174
8	134	48	26	13	18	236	72	35	23	32	16	77	26	83	132	23	12	76	141	288	79	79	59
9	24	72	32	20	8	30	428	93	35	26	18	26	50	23	56	113	21	17	108	128	323	138	89
10	16	27	71	12	11	10	25	328	82	32	14	25	21	35	14	33	94	18	22	74	116	201	137
11	12	20	12	18	4	12	21	33	348	76	21	24	24	10	20	13	24	43	17	19	74	60	156
12	15	18	11	4	5	5	6	22	25	246	51	44	18	10	10	18	14	11	53	17	19	38	55
13	6	16	6	3	1	6	27	21	7	15	190	83	27	13	10	11	11	8	16	44	24	22	27
14	3	6	9	1	0	1	0	11	7	4	10	289	20	13	6	14	8	7	8	11	26	15	15
15	0	5	5	2	0	2	0	7	4	5	4	17	283	205	90	135	86	43	51	33	59	19	21

Age	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
0	8284	2206	8533	10531	6575	3344	2738	8188	3607	2696	11814	7374	5335	7028	2588	3753	1960	2423	2546	3211	5113	1636	13722
1	232	6762	3307	6188	3544	7217	5878	1274	5642	6675	9375	9193	5773	1098	2707	5736	2974	1174	4159	4505	2000	7608	9150
2	424	32	457	499	925	261	229	67	34	253	196	234	328	242	73	288	157	91	81	167	600	400	1233
3	51	114	13	1530	358	153	123	144	72	39	307	579	260	301	79	45	164	140	123	81	276	7	39
4	34	2	50	11	18	68	226	146	100	27	3	15	6	23	34	50	56	295	483	125	185	384	61
5	153	24	7	45	57	697	233	410	359	93	22	8	51	82	35	118	59	63	1062	517	186	172	602
6	119	224	55	9	55	85	996	126	654	327	281	43	16	253	176	63	113	56	93	543	547	164	136
7	396	117	266	65	7	77	100	789	150	394	246	249	71	17	264	184	74	98	80	43	629	516	205
8	232	269	105	284	31	9	68	68	744	89	344	132	264	50	21	329	223	50	102	33	80	602	380
9	93	143	328	139	126	72	13	46	50	350	61	138	108	124	68	26	389	172	65	57	89	77	378
10	134	58	185	300	57	230	73	15	66	14	320	37	99	73	142	98	51	271	241	41	110	83	79
11	122	66	57	153	114	107	201	42	8	51	9	113	38	43	77	211	110	42	378	102	87	103	86
12	282	57	63	50	73	241	105	185	53	10	51	15	68	30	40	85	250	84	59	202	195	108	108
13	76	206	36	47	15	147	206	84	140	18	6	14	3	20	38	50	89	167	142	33	368	254	107
14	38	31	182	14	10	24	108	134	58	77	6	4	17	2	8	17	36	53	211	57	66	348	187
15	33	45	31	127	57	105	108	141	237	145	147	28	27	14	16	15	42	56	161	135	107	47	256

Table 4 *(cont.)*

Age	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
0	5697	10676	5176	5364	5002	9667	17896	12884	6208	3693	4807	3613	2303	3927	427	1784	561	119	31	347	29	66	31
1	5055	7071	2871	2024	3291	2798	1985	13581	16076	4081	2119	2728	3781	663	9877	437	507	529	43	41	4	8	4
2	581	855	510	627	220	666	326	393	2885	1041	2045	220	2854	1678	70	388	142	33	85	20	2	4	2
3	740	266	93	117	23	18	15	122	31	1844	760	115	90	2049	1392	99	188	6	2	35	2	0	3
4	47	1436	276	252	373	18	27	18	8	8	836	399	256	27	3254	1881	1	19	1	3	25	0	0
5	101	143	2045	314	154	111	26	28	4	3	5	2046	571	467	27	1387	9	1	1	4	1	25	1
6	356	236	114	2555	229	89	147	24	15	7	2	14	2200	1306	421	14	5	3	0	2	2	0	31
7	82	490	190	110	1985	194	115	96	19	20	4	2	20	2885	1132	94	1	3	1	1	0	0	0
8	111	128	275	204	72	974	241	73	62	12	18	3	15	38	1721	134	12	1	1	1	0	0	0
9	314	200	85	264	127	71	1104	204	49	59	9	25	7	14	9	345	34	13	0	0	0	0	0
10	395	440	193	131	183	123	89	1163	136	53	108	29	19	17	6	2	36	26	4	0	0	0	0
11	62	461	296	198	88	201	124	85	728	117	93	96	40	26	4	1	0	28	7	0	0	0	0
12	91	88	203	273	121	99	198	130	50	814	174	82	101	11	9	1	0	0	5	1	0	0	0
13	94	101	59	163	149	77	89	154	45	44	924	153	108	69	9	3	0	0	0	1	0	0	0
14	99	133	85	63	132	71	77	57	63	55	80	773	139	72	18	3	0	0	0	0	0	0	0
15	216	127	104	89	34	69	85	47	22	66	60	46	704	97	14	2	0	0	0	0	0	0	0

Age	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
0	20	43	20	33	7	8	23	127	34	29	14	14	15	7	1	0	2	7	0	–	–	–	–
1	2	6	2	4	1	1	1	5	2	13	1	6	3	2	0	3	0	0	0	–	–	–	–
2	1	3	1	2	0	12	0	2	2	207	3	36	9	25	16	3	1	7	8	1	30	22	83
3	23	22	3	6	6	4	14	3	4	22	540	20	63	3	19	8	13	28	33	58	34	130	70
4	5	24	12	2	6	5	8	21	5	16	18	501	25	4	3	3	33	107	110	346	714	271	242
5	0	0	20	7	2	9	5	10	62	17	15	19	550	6	12	1	5	87	364	623	1571	1796	368
6	0	0	1	11	8	2	6	6	18	130	16	4	9	324	11	15	1	9	165	638	941	1994	1760
7	13	0	0	0	16	5	2	7	13	59	105	7	4	3	226	9	12	4	16	231	406	761	1264
8	0	11	1	0	0	8	5	1	16	55	75	28	6	1	1	219	6	30	8	16	103	326	381
9	0	0	5	0	0	0	6	5	7	63	42	12	15	1	2	2	226	19	37	16	6	61	130
10	0	0	0	3	0	0	0	7	16	10	77	10	9	3	2	0	2	410	36	70	7	20	43
11	0	0	0	0	3	0	0	0	6	31	19	5	3	1	2	0	1	0	645	84	65	32	25
12	0	0	0	0	0	1	0	0	0	50	66	8	3	1	1	1	0	0	3	912	18	91	3
13	0	0	0	0	0	0	0	0	0	0	80	7	3	0	0	0	1	0	0	4	837	19	113
14	0	0	0	0	0	0	0	1	0	0	0	7	2	0	1	0	0	0	0	0	0	370	6
15	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	1	0	0	2	0	0	0	109

Table 5 Maturity at age and natural mortality (*M*).

Age	1907–49	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1
3	0.03	0	0	0	0	0	0.08	0.08	0	0.08	0.08	0.08	0.04	0	0.04	0.02	0	0.01	0	0	0.62	0.06	0.1	0	0.5	0.5
4	0.16	0.1	0.1	0.1	0.1	0.1	0.22	0.22	0	0.22	0.22	0.22	0.35	0.11	0.03	0.06	0.34	0.15	0.01	0	0.89	0.13	0.25	0.1	0.9	0.9
5	0.38	0.3	0.3	0.3	0.3	0.3	0.37	0.37	0.5	0.37	0.37	0.37	0.68	0.67	0.32	0.28	0.35	1	0.23	0.01	0.95	0.31	0.6	0.25	1	1
6	0.74	0.6	0.6	0.6	0.6	0.6	0.85	0.85	0.6	0.85	0.85	0.85	0.94	1	0.9	0.32	0.76	0.96	1	0.76	1	0.17	0.9	0.6	1	1
7	0.97	0.9	0.9	0.9	0.9	0.9	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.9	1	1
8 +	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Age	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	*M*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.9
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.9
2	0.1	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.9
3	0.5	0.5	0.73	0.13	0.1	0.25	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.4	0.1	0.1	0.01	0.01	0	0	0	0	0.15
4	1.0	0.9	0.89	0.90	0.62	0.5	0.5	0.48	0.5	0.5	0.5	0.2	0.3	0.3	0.3	0.8	0.7	0.2	0.3	0.3	0.01	0.01	0.3	0.3	0.15
5	1	1	1	1	0.95	0.97	0.9	0.7	0.69	0.9	0.9	0.9	0.9	0.9	0.9	0.9	1	0.8	0.8	0.8	0.8	0.45	0.9	0.9	0.15
6	1	1	1	1	1	1	1	1	0.71	0.95	1	1	1	1	1	0.9	1	1	1	1	1	1	1	1	0.15
7	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.9	1	1	1	1	1	1	1	1	0.15
8 +	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.15

Table 6 Stock numbers (start of year) (millions).

Age	1907	1908	1909	1910	1911	1912	1913	1914	1915	1916	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929
0	34137	42401	29953	58329	29518	53555	137317	33356	30138	88379	123043	238291	206686	198397	96452	264296	441490	100059	363592	143610	34216	135280	38086
1	19551	13371	16405	11204	22994	10294	19974	54606	11093	11164	34755	49025	95310	81336	79467	37484	106244	178669	39328	146795	55862	11213	52147
2	13945	7343	4619	5649	4227	7377	3157	7631	18701	3554	4054	13349	19211	35878	31929	30474	14666	42636	70831	15333	55975	18768	3947
3	20849	5600	2854	1544	1966	1508	2750	1198	2908	7361	1385	1521	5125	7601	14370	12862	12091	5873	17253	28716	6194	22633	7390
4	1599	17517	4362	1740	868	1354	1191	2198	918	2415	6123	1047	1195	4216	6449	12170	10675	10260	5018	14789	24598	5246	18515
5	660	1234	14997	3752	1436	745	1162	1017	1878	785	2016	5116	889	981	3602	5543	10394	9156	8808	4294	12716	20999	4440
6	630	449	1014	12714	3189	1222	632	983	855	1563	629	1623	4197	712	809	3017	4622	8571	7819	7532	3547	10829	17764
7	548	447	332	819	10706	2667	1034	516	811	710	1248	519	1283	3283	587	681	2490	3858	7079	6663	6438	2977	9174
8	1994	391	328	265	675	8972	2232	877	418	668	586	1029	414	980	2636	488	578	2056	3213	5740	5671	5494	2487
9	611	1592	291	258	216	565	7504	1854	723	338	545	489	814	332	767	2146	398	486	1699	2634	4674	4807	4656
10	295	504	1304	221	204	178	458	6062	1509	590	267	453	396	654	265	608	1743	323	403	1362	2148	3723	4010
11	218	243	415	1112	173	171	142	375	5187	976	437	210	368	319	553	210	511	1478	239	331	1154	1780	3149
12	282	339	192	347	953	144	143	117	303	4441	612	329	140	300	265	467	164	427	1262	156	269	976	1497
13	116	296	120	159	296	820	119	98	81	255	3808	351	206	95	246	219	392	131	361	1071	94	209	820
14	64	113	172	26	136	254	705	102	74	64	215	3268	34	158	70	206	175	329	106	303	912	57	166
15	0	87	94	44	21	117	218	607	81	60	51	181	2798	25	100	40	52	71	243	44	231	730	31

Age	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
0	562562	95521	225984	156732	249499	167830	99810	538598	408408	185486	212786	147108	81889	285881	250939	118827	79137	183071	107708	70029	750043	140573	96461
1	12228	226006	35977	88103	58392	98213	64868	37833	213757	163747	73694	78980	55108	29892	111749	100374	45919	30925	72886	42167	26424	301685	56110
2	16117	4823	87575	12518	31874	21481	35329	22625	14570	83310	62318	23984	26249	18724	11453	43708	37152	16773	11825	26982	14271	9468	117805
3	1441	6283	1941	35314	4771	12369	8567	14218	9156	5902	33710	25212	9602	10463	7459	4610	17587	15005	6761	4756	10864	5420	3594
4	5713	1193	5302	1658	28976	3774	10504	7259	12104	7814	5043	28729	21163	8023	8726	6347	3926	14985	12785	5705	4019	9094	4659
5	15784	4885	1024	4516	1417	24924	3186	8832	6113	10325	6700	4338	24714	18209	6885	7479	5416	3328	12624	10556	4794	3287	7471
6	3678	13444	4183	875	3846	1167	20806	2525	7221	4929	8801	5746	3726	21224	15597	5893	6327	4607	2805	9880	8606	4109	2670
7	15000	3055	11363	3549	745	3259	925	16984	2057	5608	3939	7314	4905	3192	18033	13261	5014	5341	3914	2328	8000	6900	3384
8	7734	12543	2521	9533	2995	635	2733	703	13886	1631	4462	3162	6064	4156	2732	15276	11243	4247	4506	3294	1964	6303	5460
9	2086	6442	10547	2072	7942	2549	538	2290	542	11262	1321	3521	2599	4975	3531	2331	12843	9470	3609	3784	2804	1617	4866
10	3925	1709	5412	8773	1654	6719	2128	451	1928	420	9369	1080	2902	2136	4166	2975	1983	10693	7992	3046	3204	2331	1320
11	3306	3265	1410	4605	7409	1318	5684	1645	350	1652	314	8055	825	2462	1799	3515	2470	1659	8952	6655	2584	2656	1930
12	2659	2584	2757	1155	3917	6310	911	4794	1244	252	1413	223	6919	647	2091	1512	2947	2024	1389	7355	5633	2143	2191
13	1263	2219	2033	2339	950	3357	5294	593	4049	941	201	1211	179	5953	538	1765	1254	2454	1664	1141	6143	4668	1745
14	692	1052	1881	1580	2000	809	2867	4457	386	3431	739	167	1038	138	5122	455	1503	1046	2063	1300	951	5226	3695
15	123	565	864	1590	1242	1669	598	2368	3705	112	2818	500	118	869	106	4394	378	1255	849	1626	2567	757	4454

Table 6 *(cont.)*

Age	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
0	85985	42075	24969	29861	25394	29986	412475	197508	76102	19002	168929	93900	8489	51412	3950	5190	9788	664	236	956	12726	8619	2967
1	30469	31326	10299	6851	8720	7135	6027	156288	72085	26983	5371	65617	35873	1983	18399	1334	973	3622	194	76	167	5155	3462
2	16978	9164	8228	2357	1495	1447	1117	1185	54883	19058	8368	832	24938	12174	384	1182	264	72	1135	51	5	66	2091
3	47110	6532	3181	3020	558	468	163	247	231	20474	7084	2098	198	8320	3880	111	233	17	8	407	8	1	24
4	3057	39861	5375	2651	2491	459	387	127	99	170	15912	5392	1700	87	5260	2048	4	26	9	5	318	5	1
5	3954	2588	32977	4370	2049	1798	378	308	92	78	139	12920	4271	1225	50	1508	18	2	5	6	1	250	4
6	5872	3309	2095	26486	3470	1621	1444	302	239	76	64	115	9222	3146	622	18	11	7	2	3	2	1	192
7	2171	4724	2629	1697	20426	2775	1312	1107	237	192	58	54	86	5897	1496	144	3	5	3	1	1	0	0
8	2723	1793	3611	2087	1359	15739	2208	1023	864	186	146	47	45	56	2399	238	37	2	1	2	0	0	0
9	4347	2241	1424	2853	1607	1103	12644	1677	812	686	149	109	38	25	13	469	80	21	0	0	0	0	0
10	3838	3450	1744	1147	2211	1265	883	9859	1254	653	536	120	71	25	8	3	83	38	6	0	0	0	0
11	1063	2937	2561	1321	866	1734	975	678	7406	1067	514	361	76	43	6	2	1	38	8	1	0	0	0
12	1582	857	2101	1930	953	663	1306	724	505	5699	810	356	222	28	13	2	0	0	7	1	0	0	0
13	1786	1277	656	1619	1408	708	479	940	503	388	4151	535	230	98	14	3	1	0	0	1	0	0	0
14	1329	1445	975	486	1335	1090	544	341	757	374	283	3499	0	69	18	0	0	0	0	0	1	0	0
15	2943	944	1126	743	336	1118	874	389	249	631	261	188	2969	0	0	2	0	0	0	0	0	1	0

Age	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
0	10072	5097	6198	12230	1551	1099	2338	376711	15946	98184	5418	15463	36892	92751	169037	460337	583329	88051	43515	23434	77144	2394	–
1	1187	4082	2045	2507	4952	626	442	936	153078	6461	39900	2194	6278	14989	37705	68725	187159	237163	35795	17692	9528	31365	973
2	1405	481	1656	830	1017	2013	254	179	378	62236	2619	16221	888	2551	6093	15329	27939	76093	96423	14553	7193	3874	12752
3	849	571	194	672	336	413	811	103	72	152	25171	1063	6572	355	1021	2467	6230	11358	30933	39198	5916	2905	1561
4	18	709	471	164	573	283	352	685	86	57	111	21164	896	5598	303	861	2116	5351	9750	26594	33684	5060	2380
5	0	10	589	394	139	488	240	295	570	69	35	79	17751	748	4815	258	739	1790	4506	8290	22568	28339	4104
6	2	0	9	488	333	118	412	202	245	433	44	17	51	14768	639	4134	221	631	1460	3541	6557	17991	22726
7	137	2	0	7	409	279	99	349	168	194	252	23	11	35	12410	540	3544	189	535	1104	2456	4787	13635
8	0	106	1	0	5	338	236	84	294	133	113	120	14	6	27	10471	456	3039	159	446	736	1744	3414
9	0	0	81	1	0	4	283	198	71	238	64	27	77	6	5	22	8810	387	2589	130	370	539	1198
10	0	0	0	65	1	0	3	238	166	54	147	16	12	53	5	3	17	7373	316	2193	97	313	407
11	0	0	0	0	54	0	0	3	198	128	37	55	5	2	42	2	2	12	5966	239	1823	77	251
12	0	0	0	0	0	44	0	0	2	164	81	14	43	1	1	34	2	1	10	4536	128	1509	36
13	0	0	0	0	0	0	37	0	0	2	95	9	5	34	1	0	29	1	1	6	3058	94	1215
14	0	0	0	0	0	0	0	32	0	0	2	10	1	1	29	0	0	24	1	0	3	1881	63
15	0	0	0	0	0	0	0	0	27	0	0	1	1	0	1	25	0	0	20	0	0	1126	1275

Table 7 Fishing Mortality (per year)

Year	1907	1908	1909	1910	1911	1912	1913	1914	1915	1916	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929
0	0.04	0.05	0.08	0.03	0.15	0.09	0.02	0.20	0.09	0.03	0.02	0.02	0.03	0.01	0.05	0.01	0.00	0.03	0.01	0.04	0.22	0.05	0.24
1	0.08	0.16	0.17	0.07	0.24	0.28	0.06	0.17	0.24	0.11	0.06	0.04	0.08	0.04	0.06	0.04	0.01	0.03	0.04	0.06	0.19	0.14	0.27
2	0.01	0.05	0.20	0.16	0.13	0.09	0.07	0.06	0.03	0.04	0.08	0.06	0.03	0.01	0.01	0.02	0.02	0.00	0.00	0.01	0.01	0.03	0.11
3	0.02	0.10	0.35	0.43	0.22	0.09	0.07	0.12	0.04	0.03	0.13	0.09	0.05	0.01	0.02	0.04	0.01	0.01	0.00	0.00	0.02	0.05	0.11
4	0.11	0.01	0.00	0.04	0.00	0.00	0.01	0.01	0.01	0.03	0.03	0.01	0.05	0.01	0.00	0.01	0.00	0.00	0.01	0.00	0.01	0.02	0.01
5	0.24	0.05	0.02	0.01	0.01	0.01	0.02	0.02	0.03	0.07	0.07	0.05	0.07	0.04	0.03	0.03	0.04	0.01	0.01	0.04	0.01	0.02	0.04
6	0.19	0.15	0.06	0.02	0.03	0.02	0.05	0.04	0.04	0.08	0.04	0.08	0.10	0.04	0.02	0.04	0.03	0.04	0.01	0.01	0.03	0.02	0.02
7	0.19	0.16	0.07	0.04	0.03	0.03	0.02	0.06	0.04	0.04	0.04	0.08	0.12	0.07	0.03	0.01	0.04	0.03	0.06	0.01	0.01	0.03	0.02
8	0.08	0.14	0.09	0.06	0.03	0.03	0.04	0.04	0.06	0.05	0.03	0.08	0.07	0.10	0.06	0.05	0.02	0.04	0.05	0.06	0.02	0.02	0.03
9	0.04	0.05	0.13	0.09	0.04	0.06	0.06	0.06	0.05	0.09	0.04	0.06	0.07	0.08	0.08	0.06	0.06	0.04	0.07	0.05	0.08	0.03	0.02
10	0.04	0.04	0.01	0.09	0.02	0.08	0.05	0.01	0.29	0.15	0.09	0.06	0.07	0.02	0.08	0.02	0.01	0.15	0.05	0.02	0.04	0.02	0.04
11	0.29	0.08	0.03	0.00	0.03	0.03	0.05	0.06	0.01	0.32	0.13	0.26	0.05	0.04	0.02	0.09	0.03	0.01	0.27	0.06	0.02	0.02	0.02
12	–	–	0.04	0.01	0.00	0.04	0.23	0.21	0.02	0.00	0.41	0.32	0.23	0.05	0.04	0.03	0.08	0.02	0.01	0.36	0.10	0.02	0.02
13	–	0.39	1.36	0.01	0.00	0.00	0.00	0.13	0.09	0.02	0.00	2.20	0.11	0.16	0.03	0.07	0.02	0.06	0.02	0.01	0.35	0.08	0.02
14	0.15	0.03	1.21	0.10	0.00	0.01	0.00	0.08	0.06	0.09	0.02	0.01	0.14	0.31	0.41	1.23	0.75	0.15	0.73	0.12	0.07	0.45	0.14
F-bar (5-12)	0.15	0.10	0.06	0.04	0.02	0.04	0.06	0.06	0.07	0.10	0.11	0.12	0.10	0.05	0.05	0.04	0.04	0.04	0.07	0.08	0.04	0.02	0.03

Age	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
0	0.01	0.08	0.04	0.09	0.03	0.05	0.07	0.02	0.01	0.02	0.09	0.08	0.11	0.04	0.02	0.05	0.04	0.02	0.04	0.07	0.01	0.02	0.25
1	0.03	0.05	0.16	0.12	0.10	0.12	0.15	0.05	0.04	0.07	0.22	0.20	0.18	0.06	0.04	0.09	0.11	0.06	0.09	0.18	0.13	0.04	0.30
2	0.04	0.01	0.01	0.06	0.05	0.02	0.01	0.00	0.00	0.00	0.00	0.02	0.02	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.07	0.07	0.02
3	0.04	0.02	0.01	0.05	0.08	0.01	0.02	0.01	0.01	0.01	0.01	0.03	0.03	0.03	0.01	0.01	0.01	0.01	0.02	0.02	0.03	0.00	0.01
4	0.01	0.00	0.01	0.01	0.00	0.02	0.02	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.02	0.04	0.02	0.05	0.05	0.01
5	0.01	0.01	0.01	0.01	0.04	0.03	0.08	0.05	0.07	0.01	0.00	0.00	0.00	0.00	0.01	0.02	0.01	0.02	0.10	0.05	0.00	0.06	0.09
6	0.04	0.02	0.01	0.01	0.02	0.08	0.05	0.06	0.10	0.07	0.04	0.01	0.00	0.01	0.01	0.01	0.02	0.01	0.04	0.06	0.07	0.04	0.06
7	0.03	0.04	0.03	0.02	0.01	0.03	0.12	0.05	0.08	0.08	0.07	0.04	0.02	0.01	0.02	0.02	0.02	0.02	0.02	0.02	0.09	0.08	0.07
8	0.03	0.02	0.05	0.03	0.01	0.02	0.03	0.11	0.06	0.06	0.09	0.05	0.05	0.01	0.01	0.02	0.02	0.01	0.02	0.01	0.04	0.11	0.08
9	0.05	0.02	0.03	0.08	0.02	0.03	0.03	0.02	0.10	0.03	0.05	0.04	0.05	0.03	0.02	0.01	0.03	0.02	0.02	0.02	0.03	0.05	0.09
10	0.03	0.04	0.01	0.02	0.08	0.02	0.11	0.11	0.00	0.14	0.00	0.12	0.01	0.02	0.02	0.04	0.03	0.03	0.03	0.01	0.04	0.04	0.07
11	0.10	0.02	0.05	0.01	0.01	0.22	0.02	0.13	0.18	0.01	0.19	0.00	0.09	0.01	0.02	0.03	0.05	0.03	0.05	0.02	0.04	0.04	0.05
12	0.03	0.09	0.01	0.05	0.00	0.03	0.28	0.02	0.13	0.08	0.00	0.07	0.00	0.03	0.02	0.04	0.03	0.05	0.05	0.03	0.04	0.06	0.05
13	0.03	0.02	0.10	0.01	0.01	0.01	0.02	0.28	0.02	0.09	–	0.00	0.11	0.00	0.02	0.01	0.03	0.02	0.10	0.03	0.01	0.08	0.12
14	0.05	0.05	0.02	0.09	0.03	0.15	0.04	0.03	1.09	0.05	0.24	–	0.03	0.12	0.00	0.04	0.03	0.06	0.09	0.53	0.08	0.12	0.05
F-bar (5-12)	0.04	0.03	0.03	0.03	0.02	0.06	0.09	0.07	0.09	0.06	0.06	0.04	0.03	0.02	0.02	0.02	0.03	0.02	0.04	0.03	0.04	0.06	0.07

Table 7 *(cont.)*

Age	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
0	0.11	0.51	0.39	0.33	0.37	0.70	0.07	0.11	0.14	0.36	0.05	0.06	0.55	0.13	0.19	0.77	0.09	0.33	0.23	0.84	0.00	0.01	0.02
1	0.30	0.44	0.57	0.62	0.90	0.95	0.73	0.15	0.43	0.27	0.96	0.07	0.18	0.74	1.84	0.72	1.70	0.26	0.43	1.84	0.03	0.00	0.00
2	0.06	0.16	0.10	0.54	0.26	1.28	0.61	0.73	0.09	0.09	0.48	0.54	0.20	0.24	0.34	0.72	1.86	1.28	0.13	0.97	0.78	0.10	0.00
3	0.02	0.04	0.03	0.04	0.05	0.04	0.10	0.76	0.16	0.10	0.12	0.06	0.67	0.31	0.49	3.26	2.04	0.52	0.27	0.10	0.39	0.12	0.16
4	0.02	0.04	0.06	0.11	0.18	0.04	0.08	0.17	0.09	0.05	0.06	0.08	0.18	0.41	1.10	4.60	0.27	1.46	0.14	1.21	0.09	0.06	0.23
5	0.03	0.06	0.07	0.08	0.08	0.07	0.08	0.10	0.05	0.04	0.04	0.19	0.16	0.53	0.85	4.75	0.76	0.31	0.30	0.93	0.71	0.11	0.31
6	0.07	0.08	0.06	0.11	0.07	0.06	0.12	0.09	0.07	0.11	0.03	0.14	0.30	0.59	1.31	1.83	0.60	0.69	0.29	1.64	1.38	0.65	0.19
7	0.04	0.12	0.08	0.07	0.11	0.08	0.10	0.10	0.09	0.12	0.07	0.03	0.28	0.75	1.69	1.21	0.35	1.13	0.50	1.45	0.78	0.60	0.02
8	0.04	0.08	0.09	0.11	0.06	0.07	0.13	0.08	0.08	0.07	0.14	0.07	0.44	1.31	1.48	0.94	0.42	1.22	1.77	5.90	3.80	0.00	0.01
9	0.08	0.10	0.07	0.11	0.09	0.07	0.10	0.14	0.07	0.10	0.07	0.28	0.24	0.98	1.33	1.58	0.60	1.18	4.97	4.38	0.34	–	0.01
10	0.12	0.15	0.13	0.13	0.09	0.11	0.11	0.14	0.01	0.09	0.24	0.31	0.34	1.34	1.47	1.32	0.63	1.37	1.99	0.62	0.62	–	–
11	0.06	0.19	0.13	0.18	0.12	0.13	0.15	0.15	0.11	0.13	0.22	0.34	0.84	1.07	1.06	1.27	0.66	1.58	2.32	1.72	–	–	–
12	0.06	0.12	0.11	0.17	0.15	0.17	0.18	0.21	0.11	0.17	0.26	0.29	0.67	0.55	1.27	0.68	1.24	–	1.87	1.80	–	–	–
13	0.06	0.12	0.15	0.04	0.11	0.11	0.19	0.07	0.15	0.16	0.02	–	1.05	1.57	–	2.34	0.37	–	–	0.00	–	–	–
14	0.05	0.11	0.09	0.11	0.23	0.07	0.19	0.16	0.03	0.21	0.26	0.01	–	–	2.11	–	–	0.30	–	–	–	–	–
F-bar (5-12)	0.06	0.11	0.09	0.12	0.10	0.10	0.12	0.13	0.07	0.10	0.13	0.20	0.41	0.89	1.31	1.70	0.66	1.07	1.75	2.31	1.27	0.34	0.11

Age	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
0	0.00	0.01	0.01	0.00	0.01	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	–	–	0.00
1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.01	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01
3	0.03	0.04	0.02	0.01	0.02	0.01	0.02	0.03	0.07	0.17	0.02	0.02	0.01	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.01	0.05	0.05
4	0.40	0.04	0.03	0.01	0.01	0.02	0.02	0.03	0.07	0.34	0.19	0.03	0.03	0.00	0.01	0.00	0.02	0.02	0.01	0.01	0.02	0.06	0.12
5	0.00	0.04	0.04	0.02	0.02	0.02	0.02	0.04	0.12	0.30	0.59	0.29	0.03	0.01	0.00	0.01	0.01	0.05	0.09	0.08	0.08	0.07	0.10
6	0.00	0.00	0.12	0.03	0.03	0.02	0.02	0.03	0.08	0.39	0.48	0.26	0.22	0.02	0.02	0.00	0.01	0.01	0.13	0.22	0.16	0.13	0.09
7	0.11	0.25	0.00	0.05	0.04	0.02	0.02	0.02	0.08	0.40	0.59	0.39	0.44	0.11	0.02	0.02	0.00	0.02	0.03	0.26	0.19	0.19	0.11
8	0.00	0.12	0.68	0.00	0.09	0.03	0.02	0.02	0.06	0.59	1.27	0.29	0.64	0.15	0.05	0.02	0.01	0.01	0.06	0.04	0.16	0.23	0.13
9	0.01	0.01	0.07	0.00	0.03	0.09	0.02	0.03	0.12	0.34	1.25	0.64	0.23	0.13	0.44	0.13	0.03	0.05	0.02	0.14	0.02	0.13	0.12
10	0.01	0.01	0.01	0.04	0.00	0.72	0.04	0.03	0.11	0.22	0.83	1.06	1.48	0.07	0.63	0.22	0.18	0.06	0.13	0.03	0.08	0.07	0.12
11	–	0.01	0.01	0.01	0.06	0.33	0.58	0.06	0.04	0.30	0.82	0.09	1.04	0.94	0.06	0.04	0.49	0.00	0.12	0.47	0.04	0.61	0.12
12	–	–	0.01	0.01	0.01	0.02	0.16	5.92	0.00	0.40	2.07	0.91	0.09	0.72	1.94	0.02	0.16	0.00	0.35	0.24	0.16	0.07	0.11
13	–	–	–	0.01	0.01	0.01	0.00	–	–	0.00	0.00	1.95	0.42	0.01	0.54	–	0.00	0.00	0.14	–	0.34	0.25	0.11
14	–	–	–	–	0.01	0.01	0.01	0.04	–	–	0.00	0.22	–	0.30	0.02	0.85	–	0.00	0.01	–	0.00	0.24	0.10
F-bar (5-12)	0.02	0.06	0.12	0.02	0.04	0.16	0.11	0.77	0.08	0.37	0.99	0.49	0.52	0.27	0.40	0.06	0.11	0.03	0.12	0.19	0.11	0.12	0.11

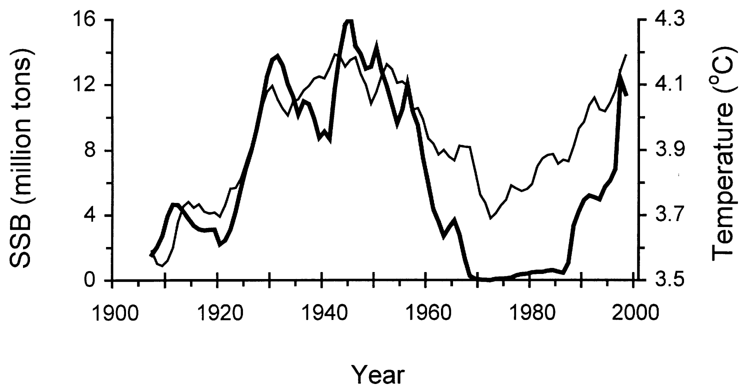

Figure 3 Fluctuations of spawning stock biomass (SSB) of Norwegian spring-spawning herring (thick line) and mean annual (moving average over 19 years) temperature (thin line) at the Kola section (Bochkov 1982), 1907-1998.

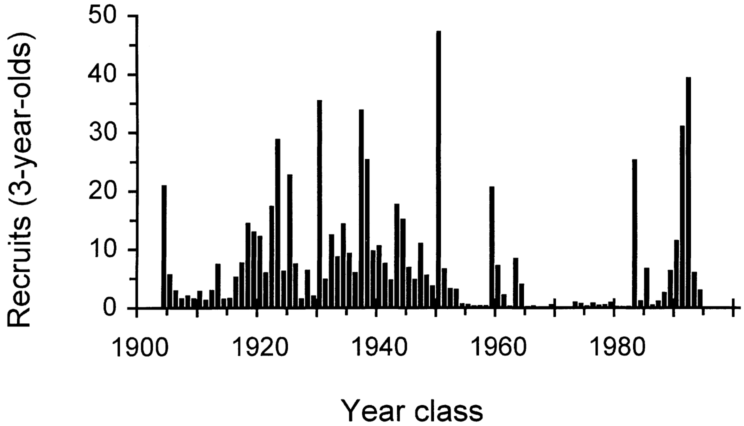

Figure 4 Number of 3 year-olds ($n \times 10^{-9}$) of Norwegian spring-spawning herring, 1904–1994.

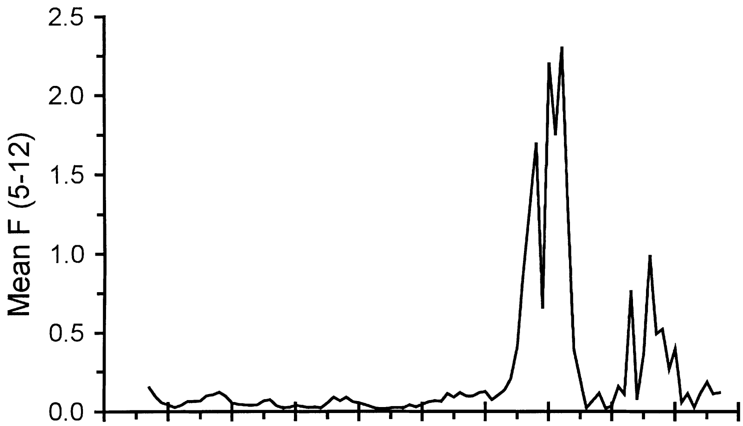

Figure 5 Mean instantaneous rate of fishing mortality (F) for age groups 5–12 years, 1907–1997.

the stock decreased while the fisheries expanded and the landings increased to a level of about 1.3 million tons. However, because of the relatively high abundance of adult herring in the stock, the mean fishing mortality was low throughout the 1950s and early 1960s. The effect of the fisheries on this stock were therefore small throughout the first 60 years of the last century. The heavy exploitation expanded even more through the 1960s (1965–67), and in 1966 the landings reached a record high figure of nearly 2 million tons. By then, the stock had been in a steady declining phase through many years. In the 1960s, the mean fishing mortality (5–12 years) therefore increased: to 0.2 in 1964, 0.4 in 1965, 0.9 in 1966 and to more than 1.3 in 1967. In 1968 the mean fishing

Table 8 Stock biomass of Norwegian spring-spawning herring ($\times$ 1000 tonnes). Bold totals (1950–98) as estimated by ICES (1999).

Age	1907	1908	1909	1910	1911	1912	1913	1914	1915	1916	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929
0	34	42	30	58	30	54	137	33	30	88	123	238	207	198	96	264	441	100	364	144	34	135	38
1	156	107	131	90	184	82	160	437	89	89	278	392	762	651	636	300	850	1429	315	1174	447	90	417
2	655	345	217	266	199	347	148	359	879	167	191	627	903	1686	1501	1432	689	2004	3329	721	2631	882	186
3	2085	560	285	154	197	151	275	120	291	736	138	152	513	760	1437	1286	1209	587	1725	2872	619	2263	739
4	318	3486	868	346	173	270	237	437	183	481	1218	208	238	839	1283	2422	2124	2042	999	2943	4895	1044	3684
5	156	292	3553	889	340	177	275	241	445	186	478	1212	211	232	853	1313	2463	2169	2087	1017	3013	4975	1052
6	168	120	270	3391	851	326	169	262	228	417	168	433	1120	190	216	805	1233	2286	2086	2009	946	2889	4739
7	157	128	95	234	3059	762	296	147	232	203	357	148	367	938	168	195	712	1102	2023	1904	1840	851	2621
8	613	120	101	82	207	2757	686	269	128	205	180	316	127	301	810	150	178	632	987	1764	1743	1689	764
9	193	502	92	81	68	178	2367	585	228	107	172	154	257	105	242	677	126	153	536	831	1474	1516	1469
10	96	163	422	71	66	58	148	1963	489	191	86	147	128	212	86	197	564	105	131	441	695	1205	1298
11	72	81	138	369	57	57	47	125	1722	324	145	70	122	106	184	70	170	491	79	110	383	591	1046
12	96	115	65	118	323	49	48	40	103	1505	207	111	47	102	90	158	56	145	427	53	91	331	507
13	40	103	42	55	103	285	41	34	28	89	1325	122	72	33	85	76	136	45	125	373	33	73	285
14	23	40	61	9	48	90	250	36	26	23	76	1157	12	56	25	73	62	117	38	107	323	20	59
15+	0	32	35	16	8	43	80	223	30	22	19	67	1028	9	37	15	19	26	89	16	85	268	12
SSB	1582	2054	2745	3937	4640	4612	4230	3776	3355	3140	3061	3107	3111	2219	2453	3125	4225	5644	6923	7972	9258	10782	12500

Age	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952
0	563	96	226	157	249	168	100	539	408	185	213	147	82	286	251	119	79	183	108	70	750	141	96
1	98	1808	288	705	467	786	519	303	1710	1310	590	632	441	239	894	803	367	247	583	337	211	2413	449
2	757	227	4116	588	1498	1289	2120	1063	728	4999	2929	1127	1234	880	538	2054	1746	788	556	1268	671	445	5537
3	144	628	194	3531	477	1596	1051	1644	794	580	3371	1513	960	1046	746	461	1759	1500	807	476	1086	542	359
4	1137	237	1055	330	5766	679	1649	1256	1956	1341	938	2936	4211	1597	1736	1263	781	2982	2485	1135	820	1855	950
5	3740	1157	243	1070	336	4618	642	1684	1132	2118	1378	854	5856	4314	1631	1772	1283	788	2819	2501	1103	756	1718
6	981	3586	1116	233	1026	288	4762	578	1558	1073	1867	1244	994	5662	4160	1572	1688	1229	781	2636	2195	1048	681
7	4286	873	3247	1014	213	891	250	4176	520	1338	981	1711	1402	912	5153	3789	1433	1526	1160	665	2200	1897	931
8	2377	3855	775	2930	920	180	813	198	3692	431	1180	854	1864	1277	839	4695	3455	1305	1375	1012	570	1828	1584
9	658	2032	3327	654	2505	778	165	673	156	3106	376	991	820	1569	1114	735	4051	2987	1095	1194	855	493	1484
10	1271	553	1752	2840	536	2057	676	142	592	123	2725	319	940	692	1349	963	642	3462	2491	986	1009	734	416
11	1098	1084	468	1529	2460	400	1852	513	108	514	99	2435	274	818	597	1167	820	551	2831	2210	840	863	627
12	901	876	934	391	1327	1948	291	1531	393	76	448	68	2344	219	709	512	998	686	452	2492	1859	707	723
13	439	772	707	814	331	1041	1719	188	1285	293	65	392	62	2071	187	614	436	854	551	397	2089	1587	593
14	245	372	666	560	708	250	945	1435	121	1059	237	54	368	49	1814	161	532	370	686	460	328	1803	1275
15+	45	208	317	584	457	536	200	759	1180	34	896	161	43	319	39	1615	139	461	296	598	929	274	1612
16+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2079	1779	1727
SSB	13525	13749	13189	12024	11275	10178	10967	10807	9951	8764	9132	8693	11737	14015	15645	16191	14379	13888	12975	13091	14267	12817	11897
SSB	**--**		**--**		**--**		**--**		**--**		**--**		**--**		**--**		**--**		**--**		**13984**	**12440**	**11482**

Age	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975
0	86	42	25	30	25	30	412	198	76	19	169	94	8	51	4	5	10	1	0	1	13	9	3
1	244	251	82	55	70	57	48	1250	577	216	43	525	287	16	147	11	8	29	3	1	2	52	35
2	798	431	387	111	70	68	52	56	2579	896	393	39	1172	572	18	56	12	3	91	4	0	6	178
3	4711	653	318	302	56	47	16	25	23	2047	708	210	20	832	388	11	23	2	1	61	1	0	4
4	624	8132	1048	544	339	94	79	26	23	37	2944	1046	316	16	947	235	0	5	2	1	82	1	0
5	909	595	7024	1005	467	435	95	83	23	23	35	2752	850	268	11	311	3	1	1	1	0	85	1
6	1497	844	545	6595	885	473	376	88	70	23	19	30	2176	698	167	5	3	2	0	1	1	0	74
7	597	1299	723	467	5352	819	380	324	72	61	18	17	22	1468	404	40	1	2	1	0	0	0	0
8	790	520	1047	605	394	4612	662	328	263	60	48	17	16	17	705	65	11	0	0	0	0	0	0
9	1326	684	434	870	490	336	3856	533	262	224	49	38	13	9	4	134	25	7	0	0	0	0	0
10	1209	1087	549	361	696	399	278	3155	404	219	179	42	26	10	3	1	27	12	2	0	0	0	0
11	345	955	832	429	281	572	317	233	2377	361	175	128	27	17	2	1	0	13	3	0	0	0	0
12	522	283	693	637	315	225	431	253	174	1904	283	127	84	11	5	1	0	0	2	0	0	0	0
13	607	434	223	551	479	244	163	348	179	135	1415	192	89	37	5	1	0	0	0	0	0	0	0
14	458	499	337	168	461	384	188	129	275	132	101	1277	0	25	8	0	0	0	0	0	0	0	0
15	1065	342	408	269	122	403	310	146	91	226	98	76	1170	0	0	1	0	0	0	0	0	0	0
16+	2687	2170	1889	1538	1022	929	547	384	152	245	222	459	163	269	51	8	2	1	0	0	0	0	0
SSB	10781	9640	10454	12017	10376	9510	7506	5946	4339	3607	2733	3220	3670	2812	1367	257	86	36	10	2	77	88	96
SSB	**10613**	**9445**	**10223**	**11740**	**10129**	**9280**	**7350**	**5817**	**4230**	**3465**	**2635**	**2795**	**3067**	**2595**	**1145**	**219**	**78**	**31**	**8**	**2**	**74**	**85**	**91**

Age	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998
0	10	5	6	12	2	1	2	377	16	98	5	15	37	93	169	460	583	88	44	23	77	–	–
1	12	41	20	25	50	6	4	9	1531	65	399	22	94	225	302	756	1310	1897	358	318	171	565	–
2	119	41	141	71	86	171	22	15	32	1431	223	892	44	255	292	567	838	1902	2411	364	180	97	319
3	154	103	35	120	59	70	138	16	10	22	1359	96	644	55	224	363	797	920	2320	2587	450	279	116
4	5	184	138	38	162	63	72	171	17	13	23	3026	121	980	60	181	474	1076	1472	3670	3975	597	350
5	0	4	192	141	48	164	73	90	168	18	9	19	3497	156	1242	63	219	474	1145	1907	4243	4931	714
6	1	0	3	188	134	45	146	74	83	135	13	5	14	3721	184	1240	72	204	464	1048	1711	4120	4931
7	56	1	0	3	172	108	38	141	63	67	86	7	4	11	3835	175	1258	67	199	382	776	1369	3300
8	0	47	1	0	2	138	93	35	116	49	41	38	5	2	11	3518	157	1088	55	173	255	563	949
9	0	0	39	0	0	2	117	87	29	94	25	9	26	2	2	8	3233	148	1066	47	138	199	364
10	0	0	0	34	0	0	1	104	69	22	56	5	4	19	2	1	6	2721	121	897	38	118	126
11	0	0	0	0	29	0	0	1	84	55	15	20	2	1	16	1	1	5	2428	99	711	30	90
12	0	0	0	0	0	22	0	0	1	70	32	5	16	1	0	15	1	0	4	1914	49	543	12
13	0	0	0	0	0	0	19	0	0	1	38	3	2	13	0	0	14	0	0	3	1217	37	418
14	0	0	0	0	0	0	0	16	0	0	1	31	0	1	13	0	0	10	0	0	1	735	24
15	0	0	0	0	0	0	0	0	12	0	0	1	26	0	1	11	0	0	9	0	0	1	463
16+	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0
SSB	150	291	364	395	480	515	514	585	613	523	454	1031	3321	4211	4917	5192	5090	4953	5726	6125	6844	12333	11426
SSB	**146**	**284**	**355**	**386**	**469**	**503**	**501**	**571**	**594**	**492**	**414**	**1031**	**3268**	**4151**	**4849**	**5119**	**5016**	**4868**	**5605**	**5948**	**6652**	**11998**	**11144**

mortality reached 1.70, reflecting the very high exploitation of adult herring through these years. The small herring were also heavily exploited through the 1960s. It is believed that the strong exploitation of the stock through the 1960s was the main reason for the following collapse of the stock (Dragesund *et al.* 1980). The total landings dropped to less than 100 000 tons in 1969 and remained low through the 1970s. From 1985 onwards, the landings increased somewhat, and the mean fishing mortality (5–12 years) increased to high levels in the mid-1980s: 0.8 in 1983, 0.4 in 1985 and 1.0 in 1986. The landings than decreased to less than 100 000 tons in 1990 and 1991. At the time, the spawning stock biomass increased and the fishing mortality therefore decreased to low levels again by 1991. Through the 1990s the total amount landed increased: to 480 000 tons in 1994 and 905 000 tons in 1995. Thereafter, in 1996–98, more than 1.2 million tons were landed. The fishing mortality has been low and less than 0.15 since 1991.

Recruitment levels and recruitment per unit of spawning stock biomass (recruitment success)

The number of recruits as 3-year-olds is shown in Fig. 4. The stock-recruitment plot is shown in Fig. 6. Of the 11 year classes, producing more than 20 billion individuals as 3-year-olds in the period from 1904 to 1994, 10 of them were produced by SSBs of larger than 4 million tons and the three most abundant year classes were produced by SSBs of larger than 10 million tons. The estimated geometric mean of recruitment as 3-year-olds for all year classes in the period 1904–94 is 2.3 billion individuals. However, the geometric mean recruitment in the years when the SSB is above 2.5 million tons is 5.1 billion individuals. The most abundant year class in the whole time range is that from 1950, estimated at some 47 billion individuals (as 3-year-olds), while the 1992 year class is the second most abundant, estimated at some 39 billion individuals.

Recruitment success is shown in Fig. 7. The number of recruits ($n \times 10^3$ 3-year-olds) per unit of SSB (tons) is estimated to be less than 7 until 1972. The number of recruits per unit SSB (r/SSB) increased to far greater numbers in three periods thereafter; in the mid-1970s, mid-1980s and in the early 1990s. In 1983, the number of recruits per SSB was more than 40, which is a very high value compared to the overall average value of 2.3 in the time series.

Relationships with ocean temperature

Trends in spawning stock biomass and mean annual temperature in the Kola section

The estimated time series of spawning stock biomass and the smoothed mean annual temperature in the Kola section (19 years smoothing) are shown in Fig. 3. A summary of a linear regression analysis of the two series and test statistics are in Table 9. The estimated correlation coefficient equals 0.82 and is highly significant ($P < 0.01$).

Recruitment and climate

The average temperatures during the winter months (January–April in the year the larvae hatch (March)) in the Kola section were correlated with the annual estimated recruitment (0-group) for the years when the estimated spawning stock was greater than 2.5 million tons. The mean temperature in the winter months was chosen because it has been shown that high temperature during winter is a proxy for increased inflow of Atlantic water to the northern parts of Norway (Fig. 1), and this increase in

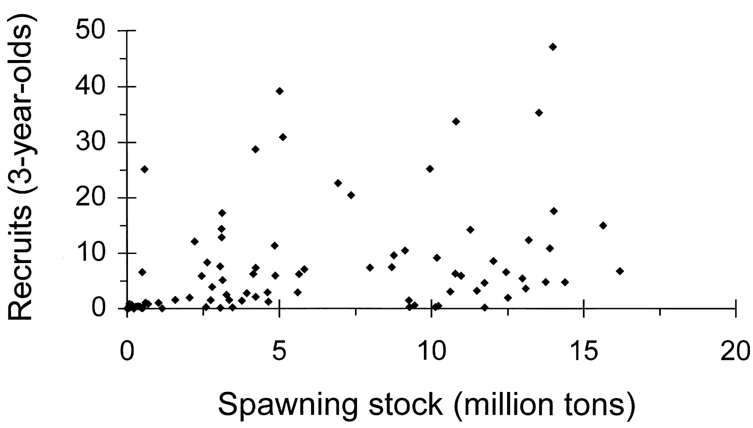

Figure 6 Spawning stock biomass (million tons) versus recruitment (3-year-olds, $n \times 10^{-9}$) of Norwegian spring-spawning herring (1904–1994).

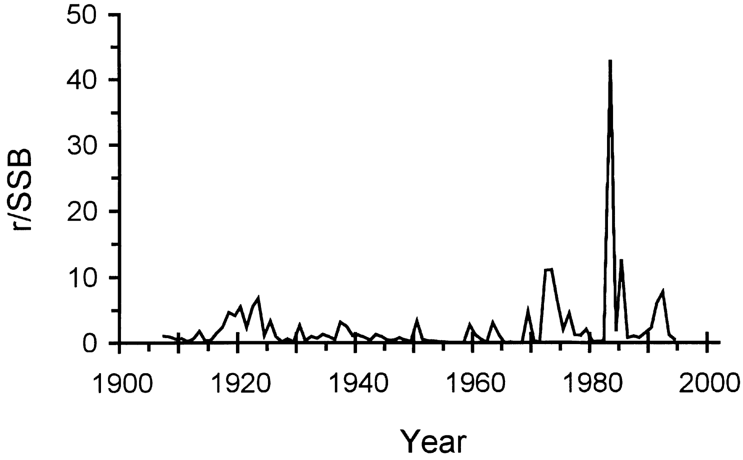

Figure 7 Recruitment (3-year-olds, thousands) per unit of spawning stock biomass (tonnes) of Norwegian spring-spawning herring, 1907–1994.

Table 9 Test statistics of correlation between absolute recruitment (unsmoothed and smoothed), recruitment success (recruits per unit spawning stock biomass; r/SSB) and SSB vs. temperature at the Kola section (Bochkov 1982) in the Barents Sea.

Series	Correlation coefficient	Significance level
Recruits—Kola (winter)	0.44	< 0.01
Recruits (smoothed, 5 years)—Kola (winter)	0.69	$<< 0.01$
r/SSB (70–98)—Kola (winter)	0.40	< 0.05
SSB—Kola (smoothed, 19 years)	0.82	$<< 0.01$

temperature has been shown to be positively correlated to year-class strength for several fish stocks in the region (Loeng 1989; Ottersen and Loeng 2000). The series are plotted in Fig. 8 and the test statistics are in Table 9. The estimated correlation coefficient is 0.44 and is significant ($P < 0.01$). The smoothed series ($q = 2$) are shown in Fig. 9. The smoothed series were also correlated and the summary statistics are given in Table 9.

The winter temperatures in the Kola section were correlated with the recruitment success (recruits per unit of SSB) for the period 1970–98. The test statistics are given in Table 9. There is a significant relationship ($P < 0.05$) between the series.

Discussion

Biological data

The relative strength of the year classes prior to 1950 are based on data from samples taken each year from the fishery on the spawning grounds. The Institute of Marine Research in Bergen organized

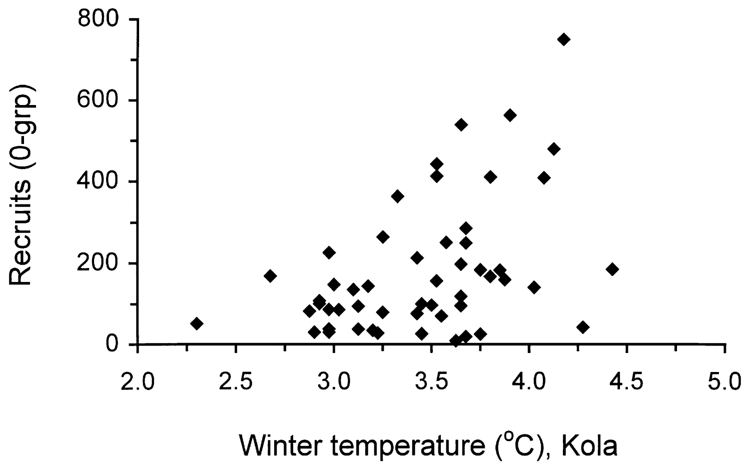

Figure 8 Number of recruits as 0-group ($n \times 10^{-9}$) versus mean winter (January–April) temperature (°C) at the Kola section (Bochkov 1982).

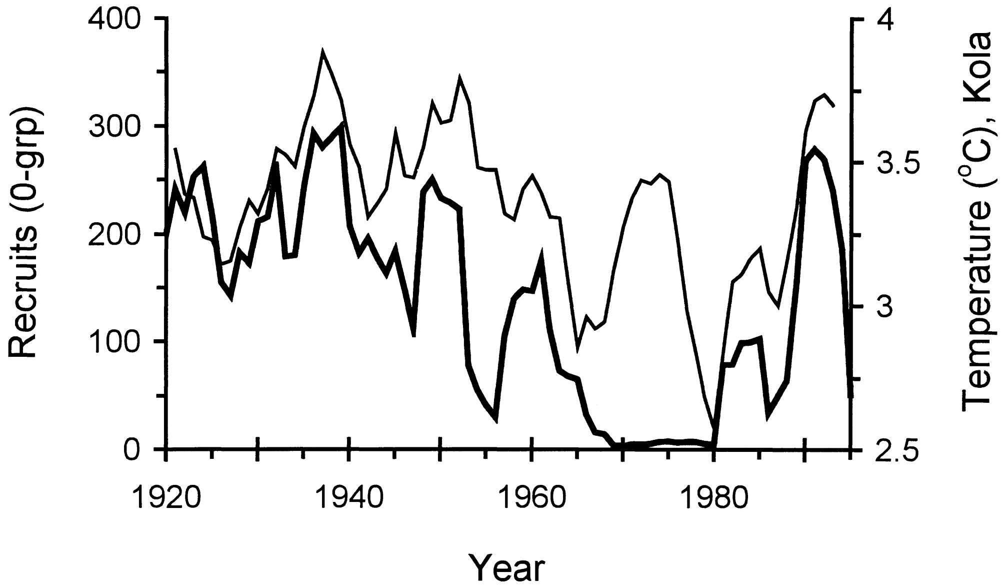

Figure 9 Time series of number of recruits (0-group) and winter (January–April) temperature (both series, moving average over 5 years) (°C) at the Kola section (Bochkov 1982).

and carried out this sampling. The fleets and fishing gear exploiting the stock have changed drastically during the 90-year period which is covered by the VPA. In the early years of this century, smaller vessels with drift nets dominated the fishery and, in addition, large catches were made by shore seines. There was a gradual change to larger vessels operating purse seines in the 1930s, followed by a very large change–the use of power blocks by the purse seine fishery–in the early 1960s. After the collapse of the stock in the late 1960s, shore seines were no longer used by the herring fishery in Norway. Drift nets have also not been used in the herring fishery since 1970. These changes in vessels and gear may have changed the proportion of the various year classes in the fishery (exploitation pattern), as the modern, larger vessels often operated more offshore than did the smaller drift net vessels and the large vessels may therefore have exploited the younger age groups of the spawning stock at an earlier age than before. The use of power blocks in the purse seine fishery, a significant change in the herring fishery, enabled the taking of larger catches using fewer men in the boats. However, the purse-seiners equipped with power blocks in the 1960s probably affected the exploitation pattern of the stock in that relatively more young individuals were caught at that time.

The quality of the biological sampling has not changed much during the 90-year period of this analysis. Scales were used for age determination from the very start of the herring investigations in 1907 and are still used for that purpose. The way the biological samples have been taken has not changed much through the years and the quality of the sampling has been equally good, at least over the last 50 years (O. Dahl, personal communication).

Method

The method for estimating numbers of fish in this VPA deviates from the official one (from 1950 to 1998) in that the number of fish at age was calculated by the use of Pope's approximation of the catch history. Hillborn & Walters (1992) showed that if total mortality is smaller than 1, the difference between the approximation and the standard way of doing the calculations is insignificant. The estimated total mortality during the early period (1907–28) is around 0.21 (Lea 1930) and thus the deviation caused by the change of method for this period is insignificant. The principles behind the calculations were the same: age group 10 was chosen to be the most representative one for the actual year class in the spawning stock (reference age) and the numbers at the other ages, cohort by cohort, were estimated by adjusting for the catch. The natural mortality is believed to be constant for the whole time series. This assumption may be wrong. Natural mortality may have been larger early in this century because the stocks of whale were larger. However, Lea (1930) arrived at an estimate of mean total mortality of 0.21 for the Norwegian herring population for the years 1907–28. Applying a natural mortality rate of 0.15 means that the fishing mortality was 0.06. This is in general agreement with the fact that the nominal catches (as seen retrospectively) were not very large (less than 500 000 tons per year), and there was a perception that the stock was large because it was easily available everywhere along the coast and in increasing amounts.

Results of the virtual population analysis

The estimated development of the stock in the period 1950–98 is endorsed by the international scientific community (ICES). The results of the present analysis are the same for this period as the one from ICES; this can be expected as it is the data from the ICES-VPA which were used as input (for the final year and oldest true age group). The question is how consistently the present VPA represent the development of the stock in the early years from 1907 to 1950? If we believe that the samples from the fisheries are representative of the relative strength of the year classes and the catch statistics indicate the exploitation of the stock, then the results should give a fairly good indication of stock fluctuations. On the other hand, if the reliability of the catch statistics has changed, and/or the sampling has changed with respect to its representation of the different cohorts in the stock, then the estimate of the development may be poorer. During the Second World War (1940–45) fish may have been landed without being reported. In addition, sampling of the catches was poor in the war period. The abundance of the year classes which were present in the fisheries during the war may therefore be biased downward. There is no reason to believe that the reliability of the catch statistics changed much before the Second World War. Neither is there any reason to believe that the samples have been more or less representative during the Second World War period.

The maximal estimate of spawning stock size, 16 million tons in 1945, is about double the estimated size of the stock today (ICES 1999). Judging from what we know about the distribution area of this stock in the 1930s and 1940s (Runnstrøm 1936; Devold 1963), both the feeding grounds and the over-wintering areas were substantially larger than today. The stock used larger areas of the Norwegian Sea for feeding and spent the winters there (Devold 1963). Because the total distribution area was much larger than it is today, it is likely that the stock was also much larger.

Climatic index

The annual mean temperature for the Kola section at 33°00′ E in the Barents Sea is a fairly good indicator of climatic fluctuations in the north-east Atlantic and is used by several authors to study the influence of temperature on fish stocks (Sætersdal & Loeng 1987; Ottersen 1996; Hamre and Hatlebakk 1998). However, this section is situated relatively far east in the inflow route of the Atlantic water masses and the mean temperature at this section may therefore be influenced by Arctic waters (Aure *et al*. 1999) and thus may, from time to time, not reflect the environmental conditions along the Norwegian coast.

Correlation of spawning stock biomass and recruitment with temperature

The correlation between the long-term development of the SSB and the temperature in the Kola section was significant. However, the temperature index series was smoothed considerably (19-years moving average) to show the long-term trend. The correlation would probably have been better if it were not for the total collapse of the spawning stock in the 20-year period from about 1965 until the mid-1980s. This collapse was probably caused by over-fishing (Dragesund *et al*. 1980).

The estimated correlation between recruitment and temperature in the Kola section was not very strong even though it is significant. There is a substantial year-to-year variation in the temperature data. When this series was filtered using a 5-year moving average, the correlation was much better.

The pattern of recruitment success in the last 30 years for north-east Arctic cod and north-east Arctic haddock (*Melanogrammus aeglefinus*, Gadidae) is one of increase during the same warm periods in the Barents Sea as was found for herring in the present work (Sundby 1994; Ottersen *et al.* 1994). The larvae and the fry of these species live in the same environment and are probably affected by common environmental factors. These factors seem to be related to heat transport by the Atlantic Current (Helle & Pennington 1999; Mukhina *et al.* 1987;

Sætersdal & Loeng 1987). Dragesund (1971) and Sætersdal & Loeng (1987) also found several cases of favourable recruitment coinciding for cod, haddock and herring stocks in the Barents Sea. These patterns are particularly striking in the last 30–40 years, a fact which is drawn attention to by Ottersen *et al*. (1994).

The underlying mechanism in the correlation between temperature and recruitment is as yet unclear. There may be both direct and indirect effects. Higher temperature has been found to affect growth positively in fish larvae (Fiksen and Folkvord 1999). Higher temperature has also been found to affect positively the production of zooplankton populations, on which the herring feed (Aksnes and Blindheim 1996). However, the pattern of the relationship between recruitment and temperature (poor recruitment at low temperatures and both high and poor recruitment at higher temperatures; see Fig. 8) indicates that the indirect effects are stronger, since high temperature is necessary for good recruitment, but it is not sufficient in itself. This feature has also been found for north-east Arctic cod (Sundby 1994).

Concluding remarks

The abundance of Norwegian spring-spawning herring has fluctuated largely during the 20th century. The spawning stock increased in biomass during the first 30 years, from a low level of about 2 million tons at the turn of the century to more than 15 million tons in 1945. It fluctuated at a high level for about 15 years until about 1950, then it decreased steadily until its collapse in the late 1960s. The stock has increased in biomass during the last 10-year period and in light of its history, it seems still to be in a rebuilding state.

Landings went through three stages before the collapse of the stock in the late 1960s. Before 1925, total landings fluctuated around 200 000 tons. There was then an increase to a level of about 600 000 tons, which lasted until about 1950. The catches increased drastically throughout the 1950s and 1960s to more than 1 million tons. After the collapse, the exploitation of juveniles and adult fish was strictly regulated. Total landings are currently on the level of about 1.2 million tons per year.

Long-term fluctuations in stock abundance seem to be governed by the influence of climate on recruitment. Sea temperature seems to be a necessary, but not sufficient condition for good recruitment. The decline in abundance through the 1950s started long before the large expansion in the fishery. However, the heavy exploitation of both young and adult herring during the 1960s seems to have been the direct cause of the collapse of the stock.

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