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Stock structure of Norwegian spring-spawning herring: historical background and recent apprehension

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For centuries, Norwegian spring-spawning herring have been the basis for a winter fishery of adult fish along the west coast of Norway. Since regular biological investigations were begun in 1907, more than half a million herring have been studied for age, length, growth, maturity, and racial characters. The present paper reviews the development of the understanding of the structure of this herring stock and how the use of age-structured data eventually became so central for both assessment and research. During the 20th century, several rich year classes contributed to the fishery. This resulted in great fluctuations in stock abundance, but structural features such as age composition, growth, and maturation also changed. Recently, a long-term virtual population analysis (VPA) was made for this stock, and trends in structural features in relation to the long-term variation in stock abundance are discussed. It was found that, even though a very large time-series was studied, the direct stock-recruitment relationship was still unclear. While recruitment seems to be governed by external factors, growth and maturation are more related to stock abundance and year-class strength.

Keywords: herring, herring stock structure, herring recruitment, herring maturation.

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Milestones of research on Atlanto-Scandian herring related to stock structural features – a brief historical review

Biology and stock structure

From the very start of the work in ICES, herring investigations became a central part, as illustrated by the terms of reference for Committee A, the so-called Migration Committee: "The migrations of cod and herring and the influence of these migrations on the fisheries especially in the northern part of the North Sea, and also the biology of these and other allied species."

Johan Hjort, the first Chair of Committee A, and his colleagues in Bergen made a fundamental contribution to fishery science through their work on representative age compositions of stocks as a tool to study stock-size fluctuations. Through the first years of the 20th century, Dahl (1907), Broch (1908), and Lea (1910) studied herring scales, and Lea became deeply involved in the investigations of the herring scale and its use for age and growth estimations and as a certificate of origin (Ruud, 1971). In 1907, a sampling programme on Norwegian spring-spawning herring was initiated. The outstanding 1904 year class of herring helped the Bergen group of scientists considerably in confirming the method of age determination by the use of scales. Since then, some five thousand individual herring have been sampled annually for scales, fat content, maturation, length, and weight (Hjort and Lea, 1911; Toresen and Østvedt, 2000).

The herring sampling programme soon gave results. Hjort and Lea discovered the new world of demography applied to fishery biology and conducted studies on length frequencies and growth types of different age groups along the Norwegian coast (Hjort and Lea, 1911). In "Fluctuations in the great fisheries of northern Europe", Hjort delivered a message saying: "By large scale stock age compositions one can identify stocks, classify them by age, measure their growth and make predictions of changes in their fishable biomass" (Hjort, 1914). The documentation from these early years confirms that scientists at the time knew the central structural features of the Norwegian spring-spawning herring. However, because of a disagreement between

British and Norwegian scientists on the use of scales and otoliths to determine age, it was not until 1923 that the question was settled and the applicability of scales and otoliths was accepted in the ICES community (Schwach, 2000; Sætersdal, 2002) and also used in the North Sea herring investigations. The use of herring scales for growth and stock structure studies and as a "certificate of origin" was fully described by Lea (1929). The studies on stock structure in the 1920s and 1930s (Lea, 1929; Runnstrøm, 1936) were fundamental in terms of establishing knowledge about the biology of Norwegian spring-spawning herring and about the separation between North Sea herring, herring in the Skagerrak, and the Icelandic herring stocks.

Lea (1929) found that the zones of the scales (the winter rings and the summer rings) had certain characteristics depending on where the herring were spawned and where they had spent their early life (at the coast or offshore). The basis for the system was that young herring in coastal areas of northern Norway and in the Barents Sea have sharp winter rings (2–6 rings) and slow growth, classified as northern type (N). Herring along the southwest coast (southern type S) have more diffuse winter rings (1–2 rings) and faster growth. An important finding was the oceanic stage (Lea, 1929). When young herring leave the coastal areas, they migrate westwards into the Norwegian Sea, where they spend one or two years, occasionally three years, before they mature and join the spawning stock.

The migratory pattern and the oceanic stage indicated by Lea (1929) seem to be in accordance with Russian investigations during the 1930s (Marty and Fedorov, 1963). These observations showed that adult herring were distributed in the central and northeastern parts of the Norwegian Sea during the feeding period.

The migratory pattern of the herring described by Lea (1929) was not complete. He was unaware of the feeding migration to the western part of the Norwegian Sea and to the area off north and northeastern Iceland. Based on extensive investigations on the herring off Iceland (*Nordurlandssild*), Fridriksson (1944) concluded that the herring caught during the summer off the north coast of Iceland consisted of three different types: Norwegian spring-spawning herring, Icelandic spring-spawning herring, and Icelandic summer-spawning herring. The Icelandic spring-spawning herring were, at least, partly identifical to the Norwegian spring spawners. He based his studies on the analysis of scales and of vertebral counts. Later tagging experiments and survey data confirmed his views (Fridriksson and Aasen, 1950, 1952; Jakobsson and Østvedt, 1999).

The two Icelandic herring stocks, the summer spawners and the spring spawners, belong to the Atlanto-Scandian herring group together with the Norwegian spring spawners (Johansen, 1919). Detailed investigations have shown that the Icelandic summer spawners differ considerably from the spring spawners in a number of morphological and physiological characters (Johansen, 1926; Fridriksson, 1944, 1958; Liamin, 1959; Einarsson, 1951). Smaller differences have been observed between the characters of the Norwegian and Icelandic spring spawners, and the Icelandic spring spawners are difficult to distinguish from the southern type of Norwegian spring-spawning herring. On the basis of growth and maturity, Østvedt (1958) concluded that Atlanto-Scandian herring are homogeneous regarding racial characters. He further concluded that the northern and the southern growth types cannot be defined as different races and that the northern type dominated rich year classes. Seliverstova (1970) related the presence of northern and southern growth types to the strength of the 1950 and 1959 year classes and found that the northern growth type dominated in the more abundant 1950 year class. She also related maturation of certain age groups in the spawning stock in 1959 to hydrological conditions.

Østvedt (1964a) presented a paper on the long-term changes in growth and maturation of Norwegian spring-spawning herring at the 1964 ICES Statutory Meeting. The paper analysed the long-term changes in mean length for different age groups. One of the conclusions was that mean length-at-age had an increasing trend through the period 1908–1963. The increase in mean length could be traced from the youngest age groups in different growth types of herring (N or S). Increases in growth were also observed in the North Sea herring stocks (Cushing and Burd, 1957) and may have been caused by common factors.

International investigations and the discovery of oceanic migration routes

The Icelandic–Norwegian tagging experiment (Fridriksson and Aasen, 1950) had proven that the Atlanto-Scandian herring migrated between the spawning grounds off western Norway and the feeding grounds at Iceland. The migration routes between the two areas were not known at the time, and soon it became of interest internationally to know these routes. On the basis of reports from the Danish research vessel "Dana" in the late 1940s, ICES recommended that countries interested in herring fisheries in the Norwegian Sea agree to a common plan of investigation in the area. In accordance with this recommendation, Denmark, Iceland, Norway, Scotland, and Sweden initiated research in the area in 1949. The surveys, which were carried out during the summer, were done annually until 1970. Joint meetings of scientists participating in the surveys were held at the end of June every year (Jakobsson and Østvedt, 1999). The investigations provided a fairly good indication of the summer distribution of Atlanto-Scandian herring in relation to temperature and plankton distribution (Østvedt, 1965).

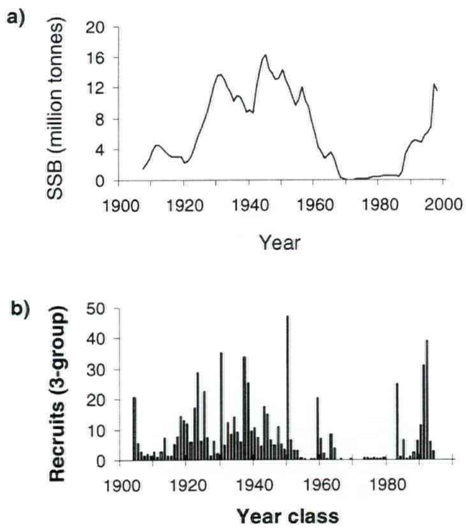

Figure 1. a) Long-term stock-size fluctuations of Norwegian spring-spawning herring, 1907–1998. b) Recruitment by year class, 1904–1994 (from Toresen and Østvedt, 2000).

First mortality estimates and studies related to factors influencing year-class strength

Lea (1930) made the first estimates of mortality of Norwegian spring-spawning herring. He based his estimates on the presence of different year classes, year after year, in samples from the stock. He found that the presence of various year classes in samples from the spawning grounds decreased at a certain rate. He found that this rate (total mortality rate of 0.21) varied little during the period 1907–1926. The exploitation of the stock was low then (Toresen and Østvedt, 2000), and the assumption that natural mortality is low (less than 0.2) for the adult portion of the stock and relatively stable seems valid.

Data on catch per unit of effort (cpue) in the Norwegian winter herring fishery were presented in a paper to the ICES Herring Symposium in 1962 (Østvedt, 1963). The results of the analysis showed a decrease in cpue after 1955 for both purse-seiners and the driftnet fishery.

A basic question in the study of Norwegian spring-spawning herring has been what factors influence year-class strength. This stock has had large variations in year-class strength, and several scientists have addressed the question (Hjort, 1914; Lea, 1930; Devold, 1963; Marty and Federov, 1963; Dragesund, 1970; Dragesund and Nakken, 1971, 1973; Barros and Toresen, 1998; Toresen and Østvedt, 2000). Dragesund (1970) considered the following factors to be most important in determining year-class strength: 1) extent of the spawning area, 2) duration of the main spawning season, 3) rate of dispersion of larvae from the spawning grounds, and 4) coincidence in time between the availability of suitable food and hatching of herring larvae. Dragesund and Nakken (1973) concluded that the results may indicate a relationship between parent stock size and subsequent recruitment when favourable conditions exist for spawning and hatching. However, they pointed out that in most years, year-class strength was determined by factors other than the size of the spawning stock. Toresen and Østvedt (2000) found that recruitment was related to temperature conditions in the inflowing Atlantic water through the Kola section and that at low temperatures, the probability of good recruitment is very low, while at higher temperatures, the probability is also much higher.

Virtual population analysis and comprehensive apprehension of stock biology

According to Hilborn and Walters (1992), the idea of summing up catches and adjusting by natural mortality has been in use at least since Ricker (1948). Fry (1949) attached the label "virtual population analysis" (VPA) to this technique, but Gulland (1965) was credited by Pope (1972) as the popularizer of VPA. In 1978, Ulltang (1977) made a comprehensive summary of the sources of errors in and limitations of the VPA.

In 1978, the first VPA of Norwegian spring-spawning herring was carried out (Dragesund and Ulltang, 1978) for the period 1950–1971. This was a turning point in the assessment work on Atlanto-Scandian herring. VPAs have subsequently been performed annually by the ICES assessment working group dealing with Norwegian spring-spawning herring, and running the VPAs has become routine (ICES, 1982, 2000). During the 1978 ICES Symposium on "The Assessment and Management of Pelagic Fish Stocks", Dragesund *et al.* (1980) made a comprehensive contribution to the biology and population dynamics of Norwegian spring-spawning herring. The paper gave a good description of the changes (and their causes) in the distribution and abundance of the stock during the period 1950–1978. The paper also contains simulations for possible developments of the stock, given different conservation strategies, through the 1960s when the stock collapsed.

An estimate of the stock trajectory of Norwegian spring-spawning herring throughout the 20th century and its relation to environmental data was made by Toresen and Østvedt (2000), who performed a VPA for the years 1907–1998 (Figure 1a,b). In general, the VPA and its later derivatives reveal inconsistencies in the applied data (for example, catch data), which make scientists more aware of their quality and variability. The use of the VPA has helped scientists working on fish population dynamics to understand how the structural features interact in a stock.

Variation in stock size and structure: what can we learn from longer time-series today?

The Norwegian spring-spawning herring is a dynamic stock which has shown large fluctuations in abundance throughout the 20th century (Toresen and Østvedt, 2000). Even though changes in stock structural features have been known for decades, and these changes have been related to variations in stock size or year-class abundance (Lea, 1930; Runnstrøm, 1936; Østvedt, 1964a; Dragesund, 1970), the stock collapse in the late 1960s and the low abundance of year classes throughout the 1970s revealed features of the stock which had not previously been seen. The growth of young herring during the 1970s was exceptionally good, and the herring reached sexual maturity at a much younger age than had been previously observed (Toresen, 1990a, 1990b).

When the long-term VPA (1907–1998) was done for Norwegian spring-spawning herring (Toresen and Østvedt, 2000), it was possible to study the long-term changes in stock structure in relation to even longer time-series of changes in stock abundance and year-class strength.

Important structural features of the spawning stock include age composition, growth, and maturation. The age composition is directly related to the occurrence of year classes of various strengths and, thereby, the recruitment process. Growth and maturation influence stock structure and are important stock-shaping features. The three elements, recruitment, growth (length-at-age), and maturation (proportion mature at age), are, therefore, chosen as key structural features to be examined in this paper.

It is generally accepted that there are certain relationships between variations in stock size and production parameters (growth and recruitment) in fish populations (Beverton and Holt, 1957; Hilborn and Walters, 1992). However, the relationship between spawning-stock size and recruitment is often obscure (Hilborn and Walters, 1992; Zheng, 1995). This may be due to several reasons, but it is likely that environmental factors influence the survival of fish larvae (Toresen and Østvedt, 2000). Another reason for a poor relation between stock and recruitment may be the use of an insufficiently long time series. For most stocks, the relationship is studied for 10–30 years. During such a period, fish stocks may change considerably in abundance, and the data points at various stock levels, therefore, are few. The biological data series are often somewhat longer than those used for stock assessment, but still short as a basis for firm conclusions. However, would the relation between stock size and stock parameters be clearer if recruitment, growth, and maturation were studied on a stock with substantially longer time series of data?

The intent of this part of the paper is to shed light on long-term changes in recruitment, growth, and maturity of the Norwegian spring-spawning herring in relation to fluctuations in stock size. The following questions are posed:

1) Is the stock-recruitment relationship for this stock different before and after the stock collapse in the 1960s?
2) When and how often did rich year classes emerge?
3) Does the age composition of the spawning stock change in relation to spawning-stock fluctuations?
4) Does length at age in the spawning stock change with total abundance of the spawning stock?
5) Do length and age at first maturity change with year-class strength?

Materials and methods

Recruitment

Recruitment and spawning-stock biomass were estimated by Toresen and Østvedt (2000). Stock-recruitment data for two periods, 1907–1972 and 1973–1997, were fitted to the Beverton and Holt (1957) stock-recruitment relationship:

$$r = \frac{\alpha \cdot S}{(1 + \frac{S}{k})}$$

where r equals recruitment, α and k are constants, and S is spawning-stock biomass. The series for the period 1907–1972 was shortened to make the two series comparable in terms of spawning-stock size range. The years with estimated stock sizes in excess of 9 million t were omitted.

Mean recruitment per unit of spawning-stock biomass and its standard deviation was calculated for four periods of spawning-stock development: 1907–1932, 1933–1945, 1946–1972, and 1973–1997. Rich, average, and poor year classes were defined, respectively, as: 1) more than 15 billion individuals, 2) between 7 and 15 billion individuals, and 3) less than 7 billion individuals as 3-year-olds, as estimated by Toresen and Østvedt (2000). The number of rich year classes in the spawning stock each year was defined as those with a biomass of more than 200 000 t.

Growth

The mean lengths-at-age in the spawning stock in February–April each year were used as indicators of changes in growth. The mean length anomaly from the long-term mean (cm) of 6-year-olds was chosen as a reference for growth anomalies. As pointed out by Runnstrøm (1936), Østvedt (1964b), and Toresen (1990a), growth anomalies in the year classes are established early in life and persist through the first years

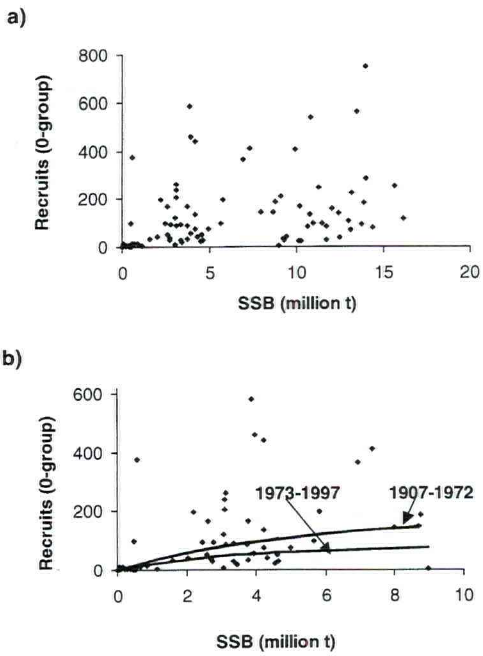

Figure 2. a) Stock-recruitment plot for Norwegian spring-spawning herring, 1907–1997. b) Beverton and Holt stock-recruitment models for the periods 1907–1972 and 1973–1997.

after maturation. The data are based on individual length-at-age measurements entered in the database at the Institute of Marine Research in Bergen, Norway.

Age at first maturity

Age at first maturity was determined in the period 1935–1973 from samples of the spawning stock by applying the cumulative frequency of the number of spawning zones in the scales for the 9-year-olds. The time-series of the proportion mature at age for the 1932–1965 year classes is presented in this paper.

Length at second time of spawning

The length at second time of spawning was used as a proxy for the length at first maturity and is defined as the mean length of the fish from samples on the spawning grounds with one spawning ring on the scales. The length at second time of spawning as 5-year-olds was correlated with the corresponding year-class strength.

Results

Stock recruitment

The Beverton and Holt stock-recruitment constants α and k were estimated to be 39.0 and 6578.0, respectively, for the period before the collapse and 29.0 and 3818.4, respectively, for the period after the collapse. The data for the first period fit best to the model with a minimum sum of squares of 6.95, while the latter period had a minimum sum of squares of 10.92.

The stock-recruitment plot for the whole time-series, 1907–1997, is shown in Figure 2a, and the estimated fits to the Beverton and Holt stock-recruitment model for the periods 1907–1972 and 1973–1997 are presented in Figure 2b. The difference between the two periods was not tested statistically, but is assumed not to be significant because most of the data points are outside the two lines.

The mean number of recruits (thousands) per unit of spawning-stock biomass (SSB) (tonnes) for each of the four main phases of spawning stock development through the 20th century is given in Table 1. Phases 1 and 4 are periods with increasing SSB, phase 2 is a period of high levels of SSB, while phase 3 is a period of decreasing SSB. The mean recruitment per unit of SSB (Table 1) varies considerably between periods and is higher during the two periods of increasing SSB than during the other two periods. The period with the smallest mean SSB has the highest mean recruitment per unit of SSB. Based on the standard deviations, the differences are not statistically significant.

Occurrence of rich and poor year classes versus spawning-stock biomass

The number of strong year classes, in 10-year periods, are presented in Figure 3. There is a significant ($p<0.01$) positive correlation between the occurrence of rich year classes and SSB within these periods, with an r^2 of 0.42. There is a significant ($p<0.01$) negative correlation between SSB within the periods and the occurrence of poor year classes ($r^2 = 0.37$).

Spawning-stock biomass age composition

The number of year classes in the spawning stock with a biomass of more than 200 kt and the estimated number of 0-group fish during the period 1907–1997 are illustrated in Figure 4. The number of year classes with a biomass above 200 kt follows the development of the spawning-stock biomass and increases steadily from one in 1907 to 13 in the mid-1950s. Thereafter, the number decreases to zero by 1970, remains at zero until 1987, and then increases again so that by 1998, there are six year classes in the spawning stock with more than 200 kt of biomass. This number was significantly correlated (positive) with recruitment ($r^2 = 0.09$).

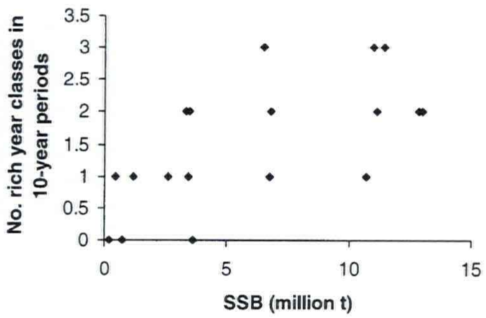

Figure 3. Number of strong year classes in 10-year periods versus spawning-stock biomass for Norwegian spring-spawning herring.

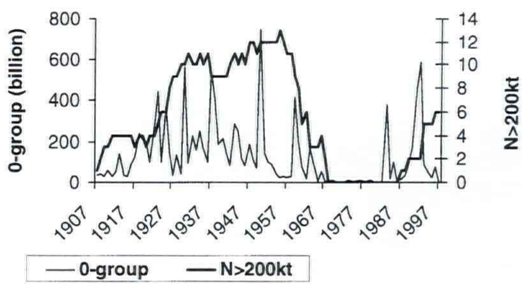

Figure 4. Number of year classes with biomass more than 200 kt and recruitment (3-year-olds) for Norwegian spring-spawning herring.

Mean length-at-age

The length distribution in the spawning-stock biomass by year at 10-year intervals during 1907–1997 is presented in Figure 5, indicating a clear shift over time. During periods of high stock production, the distribution is broad and the occurrence of the recruiting year classes is readily seen in the distributions, while during periods of poor recruitment (1967 and 1977), the distributions are more narrow and smaller fish are not seen. In the late 1980s, there is a clear shift towards smaller fish in the spawning stock, indicating relatively good recruitment.

Mean length in the spawning stock during the years 1907–1997 is shown in Figure 6. Because samples from the spawning grounds often contain younger fish as well, mean length in the spawning stock is calculated from fish >29 cm as this has been estimated to be the overall length at first maturity for Norwegian spring spawners (Beverton, 1992). There is a tendency for increased mean length in the spawning stock through the period. However, a more striking feature is the increased variance of the mean length after about 1960, a feature still present in the stock.

Table 1. Four periods or main phases of the Norwegian spring-spawning herring through the 20th century with the mean spawning-stock biomass (SSB), mean recruitment per unit of SSB (thousands per t), and the standard deviation (S.d.).

Number	Period	Mean SSB (kt)	Mean r/SSB	S.d.
1	1907–1932	5 727	1.91	1.9
2	1933–1945	11 491	1.17	0.8
3	1946–1970	7 484	0.85	1.3
4	1975–1995	2 141	4.40	9.6

Age 6 was chosen as a reference age for growth anomalies. As pointed out by Runnstrøm (1936) and Toresen (1990a), growth anomalies in the year classes are established early in life and persist through the first years following maturation. The time-series of the anomalies in annual mean length-at-age 6 is presented in Figure 7 together with the SSB time-series. The two series were tested and showed a negative correlation with $r^2 = 0.3$, however, not significant ($p>0.05$). The time-series of length-at-age anomaly for 6-year-olds was also correlated with the strength of the respective year classes. The correlation was significantly ($p<0.01$) negative ($r^2 = 0.08$).

Growth types

In this study, the number of northern and southern growth-type fish in the 1933–1954 year classes were correlated with the recruitment of the respective year classes in a multiple regression. A significant ($p<0.01$) positive relation ($r^2 = 0.34$) was found between the number of northern-type herring and recruitment as 0-group herring, while the relation between southern-type herring and recruitment was very weak and not significant. This indicates that rich year classes have, in their young stages, been distributed either at the northern coast of Norway or in the Barents Sea. This feature was also noted by Runnstrøm (1936), Østvedt (1965), and Marty (1956).

Maturity by age and length

The proportion mature-at-age for the 1926–1964 year classes is given in Table 2. The time-series of the percentage of maturity of a year class by 5-year-olds was

Table 2. Proportion maturity-at-age for the 1926–1964 year classes.

Age	1926	1927	1928	1929	1930	1931	1932	1933
2	-	-	-	-	-	-	-	-
3	-	-	0.04	-	-	-	-	-
4	0.01	-	0.21	0.10	-	0.13	0.04	0.04
5	0.24	0.60	0.50	0.30	0.26	0.38	0.20	0.12
6	0.93	1.00	0.88	0.80	0.78	0.75	0.56	0.40
7	0.99	1.00	1.00	1.00	0.98	0.99	0.85	0.84
8	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	1934	1935	1936	1937	1938	1939	1940	1941
2	-	-	-	-	-	-	-	-
3	-	-	-	-	0.01	0.05	0.02	0.08
4	0.05	0.06	0.10	0.01	0.05	0.16	0.26	0.26
5	0.14	0.18	0.18	0.08	0.18	0.48	0.62	0.83
6	0.30	0.33	0.46	0.67	0.71	0.86	0.97	1.00
7	0.68	0.74	0.98	0.98	0.99	1.00	1.00	1.00
8	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	1942	1943	1944	1945	1946	1947	1948	1949
2	-	-	-	-	-	-	-	-
3	0.12	0.10	0.11	0.22	0.11	0.03	0.01	0.07
4	0.47	0.35	0.50	0.72	0.47	0.24	0.08	0.30
5	0.91	0.77	0.97	0.94	0.91	0.58	0.28	0.80
6	0.99	1.00	0.99	1.00	0.99	0.87	0.91	0.97
7	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
8	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	1950	1951	1952	1953	1954	1955	1956	1957
2	-	-	-	-	-	-	-	0.17
3	0.03	0.06	0.06	0.07	0.07	-	0.50	0.50
4	0.21	0.39	0.42	0.30	0.45	0.43	0.75	0.67
5	0.50	0.74	0.87	0.55	0.86	1.00	1.00	0.92
6	0.62	0.79	0.96	0.94	1.00	1.00	1.00	1.00
7	0.78	0.96	1.00	1.00	1.00	1.00	1.00	1.00
8	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	1958	1959	1960	1961	1962	1963	1964	
2	-	-	-	-	-	-	-	
3	-	0.01	0.01	-	-	-	-	
4	0.25	0.14	0.13	0.51	0.55	0.25	0.07	
5	0.75	0.51	0.60	0.82	0.93	0.50	0.14	
6	1.00	0.97	0.91	1.00	1.00	0.75	0.43	
7	1.00	1.00	1.00	1.00	1.00	1.00	0.79	
8	1.00	1.00	1.00	1.00	1.00	1.00	1.00	

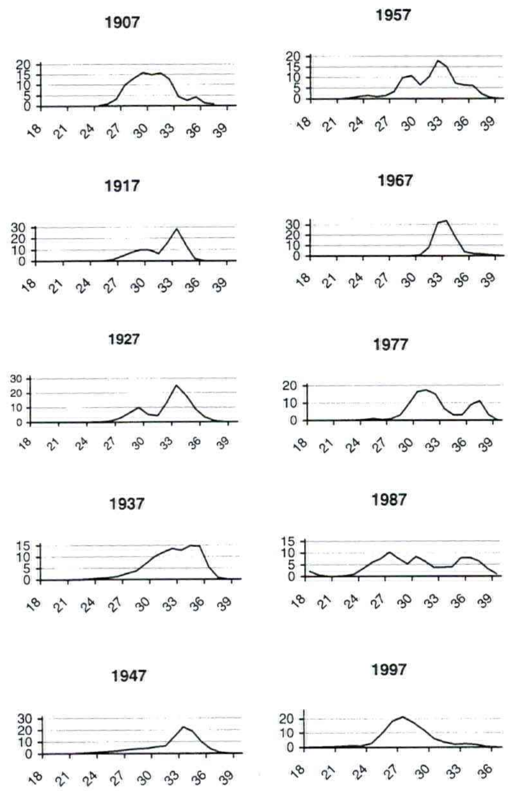

Figure 5. Length distribution in the spawning-stock biomass of Norwegian spring-spawning herring in years at 10-year intervals, 1907–1997.

correlated with the corresponding time-series of year-class strength (Figure 8). The regression between the two series showed a significant ($p<0.05$) negative correlation ($r^2 = 0.16$). This means that the stronger the year class, the later the maturation, which is in agreement with Marty's (1956) observations of the slow growth and late maturation of the northern growth-type of Atlanto-Scandian herring. A linear regression between the length at second time of maturity of fish as 5-year-olds and year-class strength showed a significant negative relation ($p<0.01$, $r^2 = 0.31$) (Figure 9). This means that the stronger the year class, the smaller the mature fish at a certain age.

These results indicate that year-class strength influences the maturity process. The more abundant the year classes, the slower the growth and the longer it takes before the fish reach maturation size.

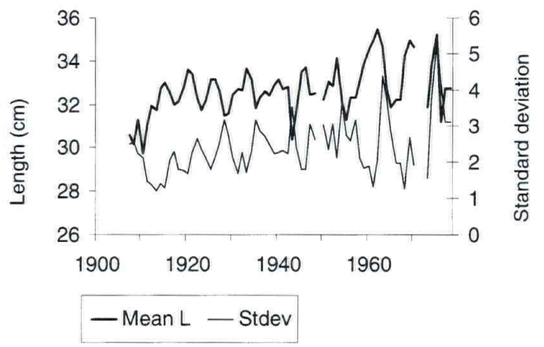

Figure 6. Mean length in the spawning-stock biomass of Norwegian spring-spawning herring, 1907–1980, for fish greater than 29 cm.

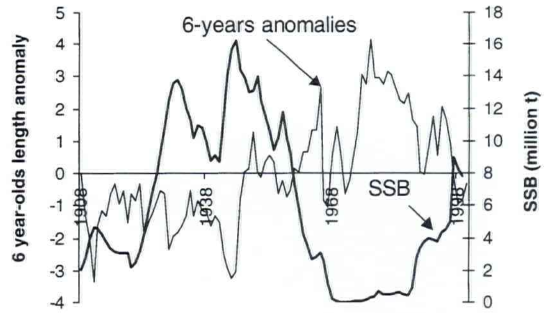

Figure 7. Anomalies in annual mean length-at-age 6 and spawning-stock biomass of Norwegian spring-spawning herring.

Discussion

Long-term fluctuations in stock size, recruitment, growth, and maturation have been observed. An interesting question is what determines these fluctuations? Are changes in recruitment and growth directly related to stock-size fluctuations or are they influenced by external, environmental factors?

Recruitment

In the study of stock-recruitment relationships, it is very rare to find examples of clear relations between spawning stock size and corresponding recruitment (Hilborn and Walters, 1992; Zheng, 1995). Most often, the relationship between stock and recruitment exhibits a very large variance, i.e., the same stock size may produce a variety of year-class abundances. Because of the very large variance in the stock-recruitment relationship for Norwegian spring spawners and the large difference in the number of observations before and after the collapse, it is impossible to draw any firm conclusions about changes in the stock-recruitment relationship before and after the stock collapse. However, the stock seems to have higher recruitment at lower stock levels in recent years. For many stocks, historical data show that below certain levels of spawning-stock biomass, it is more likely that recruitment may fail. For Norwegian spring-spawning herring, the lower SSB limit is estimated to be 2.5 million t (ICES, 2000). There seems to be a breakdown in recruitment at stock levels below this level (Figure 2). However, the stock has shown that it is capable of producing rich year classes at a much lower level, such as in 1983, when the spawning-stock size was estimated at only 600 000 t and one of the richest year classes in the century was produced (Toresen and Østvedt, 2000).

Further on, a positive correlation was found between the number of rich year classes in the spawning-stock and spawning-stock biomass itself. This is in accordance with the fact that even though the direct relationship between stock and recruitment is poor, the relation becomes clearer if the data are grouped, and during periods when the spawning stock is greater, there is a higher possibility of better recruitment. However, this may be an artificial effect of the spawning stock level. In recent studies (Toresen and Østvedt, 2000), it has been shown that there is a positive relationship between environmental factors and recruitment in Norwegian spring-spawning herring. During periods of high stock levels, environmental conditions have been favourable for good recruitment, and this effect may prevail for a longer time owing to long-term fluctuations in climatic conditions.

There also seems to be a relationship between the spawning-stock age composition and recruitment. If there are few dominant year classes, recruitment is poorer than if there are more dominant year classes. A broad distribution of the biomass between year classes in the spawning stock may increase the possibility of rich year classes as the different group types or cohorts often spawn at different times and locations. A spread of larvae over time and space may favour survival and improve recruitment. On the other hand, rich year classes consist of high numbers of maturing cohorts. The very large 1950 year class, which consisted of subgroups with different growth histories during younger stages, matured to spawn between 3 and 9 years of age. This would have an effect similar to the occurrence of several strong year classes in the spawning stock. The positive relation between recruitment and the age composition in the spawning stock may, therefore, be artificial and instead reflect the results of an environmental influence.

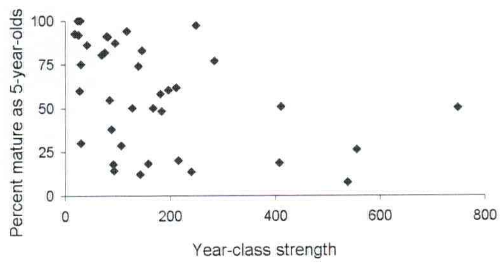

Figure 8. Year-class strength (billions of individuals at the 0-group stage) versus percentage mature fish of a year class as 5-year-old Norwegian spring spawners (1935–1973).

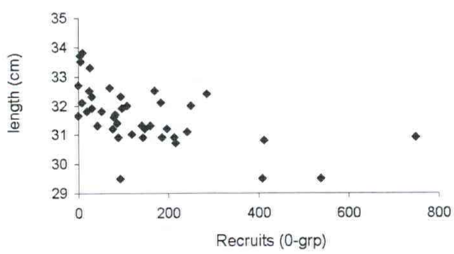

Figure 9. Year-class strength (billions of individuals at the 0-group stage) versus length (cm) of mature fish as 5-year-old Norwegian spring spawners (1935–1973).

Length-at-age

The relationship between length-at-age, stock size, and year-class strength is ambiguous. On one hand, there is a negative relation between length-at-age and stock size. However, even though there is a relationship, it is hardly statistically significant at the 5% level. There is also a negative relation between length at age and year-class strength, but that relation is even poorer. Earlier studies, such as by Toresen (1990a), have found negative correlations between growth and year-class strength of Norwegian spring-spawning herring. However, it has also been shown that high temperatures favour both recruitment and individual growth (Toresen and Østvedt, 2000; Holst, 1996). It is unclear whether abundance-dependent reduction in growth overrules temperature-dependent increase in growth. However, the Norwegian spring spawners are distributed over a very large area (Lea, 1929), and the two dominating effects may influence growth in various ways, depending on the relative strength of the different components of the stock and the distribution of the young age groups.

Growth types and maturation

It is clear from the results that the maturation process is influenced by growth. In general, rich year classes mature later than poor year classes. This is in agreement with earlier studies (Runnstrøm, 1936; Østvedt, 1958; Toresen, 1990b) where it was concluded that the maturation process is dependent on the size rather than the age of the herring, and Beverton (1963) found that a mean maturation length exists for herring which is about 75% of the L_∞ The L_∞ for Norwegian spring-spawning herring is estimated to be 39 cm (Beverton, 1963), giving a maturation length of 29.25 cm. In the present study, length at first maturity was also found to vary with year-class strength, and strong year classes mature at an older age and at a somewhat larger size than weaker year classes. This is in agreement with the findings of Østvedt (1964a).

Concluding remarks

Long-term changes in stock structural features such as recruitment, length-at-age, and maturation have been determined and found to be related to the huge changes in spawning-stock biomass of Norwegian spring-spawning herring.

Norwegian spring-spawning herring have an unclear stock-recruitment relationship. With spawning stock size above 2.5 million t, the stock-recruitment relationship seems random. However, a positive relationship was found between recruitment and the age composition of the spawning stock in terms of the number of year classes in the stock above 200 kt. There also seems to be an increasing frequency of rich year classes with increasing spawning-stock biomass. These features were clear in the 1930s and 1940s. However, all in all, the recruitment level seems to be determined by external environmental factors rather than stock size.

There is a negative correlation between year-class strength and the growth anomaly as 6-year-olds. There is also a negative relation between the growth anomaly and spawning-stock biomass. In other words, there was a period of enhanced growth during the period of low stock abundance in the 1970s and early 1980s.

Rich year classes mature to spawn at an older age than poor year classes, mainly because of poorer growth. Poor year classes mature at a younger age and at a somewhat smaller size than rich year classes. During the period of stock collapse, the age at first maturity was significantly lower than during earlier or later periods.

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