STOCK SIZE FLUCTUATIONS AND RATE OF EXPLOITATION OF THE NORWEGIAN SPRING SPAWNING HERRING, 1950—1974

By
OLAV DRAGESUND
Department of fisheries biology,
University of Bergen
and
ØYVIND ULLTANG
Institute of Marine Research, Bergen

ABSTRACT

DRAGESUND, O. and ULLTANG, Ø. 1978. Stock size fluctuations and rate of exploitation of the Norwegian spring spawning herring, 1950—1974. *FiskDir. Skr. Ser. HavUnders., 16*:315—337.

The collapse of the Norwegian spring spawning herring stock is described, followed by a discussion of the causes. Stock size and fishing mortality were calculated from virtual population analysis for the years 1950—1974. The analysis showed that the young herring fishery had a serious effect on the recruitment to the adult stock during the whole period. The 1961 year class was the last one which survived the small- and fat-herring fisheries in any quantity.

The fishing mortalities on the adult stock were at a low or moderate level until 1964. Thereafter a rapid increase in the fishing mortalities took place, primarily as a result of the escalation in the summer and autumn fisheries off Iceland.

The result of the investigation leaves no doubt that the fishing pressure was the primary factor for the collapse of this herring stock.

INTRODUCTION

Traditionally the main fishery on the adult stock of Norwegian spring spawning herring took place in winter along the Norwegian west coast prior to and during the spawning season (DEVOLD 1963). Another important fishery, the summer and autumn herring fishery, took place on the feeding grounds along the Polar front in the Norwegian Sea. This fishery was for a long period located off northern and northeastern Iceland exploiting mainly the adult stock (JAKOBSSON 1963). During the last two decades there has been a drastic change in the migration pattern of the adult stock, and this has strongly influenced the location of the summer and autumn as well as the winter herring fishery (DEVOLD 1968, JAKOBSSON 1968).

Although the total catch of adult herring (including the summer and

Table 1. Total catch in thousand metric tons of adult Norwegian spring spawning herring
1950—1971.

Year	Iceland	Norway	USSR	Faroes	Fed. Rep. of Germany	Total
1950	30.7	781.4	14.0	—	—	826.1
1951	48.9	902.3	43.0	—	—	994.2
1952	9.2	840.1	69.9	—	—	919.2
1953	31.5	692.2	110.0	16.2	—	849.9
1954	15.2	1 103.6	160.0	27.6	—	1 306.4
1955	18.1	979.3	207.0	13.1	—	1 217.5
1956	41.2	1 160.7	235.0	23.7	—	1 460.6
1957	18.2	813.1	300.0	17.0	—	1 148.3
1958	22.6	356,7	388.0	17.7	—	785.0
1959	34.5	426.9	408.0	13.7	—	883.1
1960	26.7	318.4	465.0	11.0	—	821.1
1961	85.0	111.0	285.0	16.9	—	497.9
1962	176.2	156.2	209.0	9.8	—	551.2
1963	177.5	130.4	350.0	12.9	—	670.8
1964	367.4	366.4	365.8	18.3	—	1 117.9
1965	540.0	259.5	489.2	31.5	5.6	1 325.8
1966	691.4	497.9	447.4	60.7	26.1	1 723.5
1967	359.3	423.7	303.9	34.9	9.7	1 131.5
1968	75.2	55.7	124.3	16.1	1.8	273.1
1969	0.6	15.6	3.2	4.4	0.3	24.1
1970	—	20.3	—	0.6	—	20.9
1971	—	6.9	—	—	—	6.9

autumn fishery) has to a large extent fluctuated in relation to the entrance of strong year classes throughout the history of the fishery (ØSTVEDT 1963), this phenomenon has been especially pronounced during the period 1950—1970 (ANON. 1970). Thus the very rich 1950 year class caused high catches in the adult herring fisheries in the mid 1950s, and the strong year classes of 1959 and 1960 gave high yields in the years 1964—1967 (Table 1). Both periods of high catches were followed by a decline which was most striking in the latter period when the decrease in the adult stock was accelerated by an increase in exploitation rate compared to earlier periods. However, the decline was primarily caused by practically no recruitment to the adult stock after the 1959 and 1960 year classes were fully recruited to the stock in 1966.

From 1965 onwards a rapid decrease in the stock size took place, and in 1969—1971 the catches in both the adult summer and winter herring fisheries were negligible compared with those of earlier years. During the spawning season of 1972 almost no herring were recorded on the traditional spawning grounds, and the spawning stock was reduced to an extraordinari-

Table 2. Catches in thousand metric tons of small and fat herring taken by Norway and USSR 1950—1974. Herring caught south of Stad are excluded except for Norwegian small herring catches in 1950—1959.

Year	Small herring			Fat herring			Grand total
	Norway	USSR	Total	Norway	USSR	Total	
1950	72.9	—	72.9	29.7	4.3–	34.0	106.9
1951	190.1	10.5	200.6	80.5	2.5	83.0	284.2
1952	276.4	2.1	278.5	55.2	1.9	57.1	335.6
1953	147.0	3.8	150.8	84.7	5.2	89.9	240.7
1954	190.1	8.8	198.9	138.0	1.2	139.2	338.1
1955	94.3	3.0	97.3	36.0	9.0	45.0	142.3
1956	86.8	—	86.8	102.0	10.0	112.0	198.8
1957	118.5	3.8	123.3	46.4	1.5	47.9	171.2
1958	133.5	8.1	141.6	55.1	4.6	60.0	201.6
1959	164.5	7.2	171.7	46.8	9.5	56.3	228.0
1960	212.0	5.7	217.7	62.2	0.8	63.0	280.7
1961	222.7	0.9	223.6	108.5	0.1	108.6	332.2
1962	124.5	0.7	125.2	171.3	0.9	172.2	297.4
1963	157.9	—	157.9	143.8	12.0	155.8	313.7
1964	106.8	—	106.8	56.9	0.2	57.1	163.9
1965	116.9	—	116.9	94.3	10.7	105.0	221.9
1966	61.7	—	61.7	147.9	21.9	169.8	231.5
1967	107.1	—	107.1	346.0	92.6	438.6	545.7
1968	26.3	—	26.3	341.1	71.7	412.8	439.1
1969	14.4	—	14.4	21.2	8.1	29.3	43.7
1970	5.2	—	5.2	36.2	—	36.2	41.4
1971	1.1	—	1.1	13.1	—	13.1	14.2
1972	3.3	—	3.3	9.9	—	9.9	13.2
1973	0.3	—	0.3	6.6	—	6.6	6.9
1974	0.6	—	0.6	5.7	—	5.7	6.3

+ Average catch for the period 1941—1950.

ly low level. In 1973—1975 a slight increase in the spawning stock took place due to recruitment from the 1969 year class. (Anon. 1974, 1975 a, 1976.)

In addition to the fishery on adults there was a fishery on young and adolescent herring in the Norwegian fjords, mainly in northern Norway. This fishery is based on the small-herring (småsild), i. e. mainly 0- and I-group fish, and on the fat-herring (feitsild), i. e. I- to IV-group herring (Dragesund 1970). The catches of small-herring have declined since the mid 1960s (Table 2). This decline was largely determined by the low abundance of small-herring due to a series of weak to moderate year classes after 1965. Catches of the fat-herring increased considerably in the years 1966–1968 after having fluctuated with no definite trend in the years 1950—1965 (Table 2).

The description of the collapse of the stock of Norwegian spring spaw-ning herring is well documented in several reports (ANON. 1970, 1972, 1975 b). The aim of the present paper is to give an analysis of the effect of the fishery on the stock during the period 1950—1974.

MATERIALS AND METHODS

Stock size and fishing mortality were calculated from Virtual Population Analysis (VPA), the main input data being the total catch in number by age in the different years. Catches in weight were converted separately to catch in number by age for the adult fisheries and the young and adolescent herring fisheries (small- and fat-herring).

The catch in number by year class in the adult fisheries from 1962 to 1970, given by the Working Group on Atlanto-Scandian Herring (ANON. 1970, 1972), was extended to cover the period 1950—1971 and all age groups in the adult fisheries (Table 3) by utilizing:

 (i) Data on age composition in the winter fishery 1950—1970 and the summer and autumn fishery 1962—1970 given in ANON. (1970, 1972).

 (ii) Data on mean weight of herring from the winter fishery 1950—1961 available from the records of Institute of Marine Research, Bergen.

(iii) Icelandic data on age composition in the summer and autumn fishery in 1950—1961 as reported in Annales Biologiques (ANON. 1951—1954, ANON. 1956—1963).

(iv) Icelandic data on mean weight by age during the summer and autumn fishery (JACOBSSON, personal communication).

 (v) Data on age composition and mean weight in catches from the Norwe-gian winter fishery 1971.

The catch in number by year class in the young and adolescent herring fisheries in 1950—1974 (Table 4) were obtained by utilizing:

 (i) Data on catch by year class in the small-herring fishery given in DRAGE-SUND (1970) and data from the records of the Institute of Marine Research, Bergen.

 (ii) Data on age composition in the fat-herring fishery given in DRAGESUND (1970) and data from the records of the Institute of Marine Research, Bergen.

(iii) Data on mean weight by month and district for year classes going through the small- and fat-herring fisheries from the 0-group to the adolescent stage given in DRAGESUND (1970).

A constant natural mortality of M=0.16, as estimated by the Working Group on Atlanto-Scandian herring (ANON. 1970), was assumed for the whole period 1950—1974 for all age groups. The Working Group arrived at the estimate by utilizing data on catch in number by age for 4 years old and older herring. It is, therefore, uncertain how representative the figure 0.16 is for younger age groups.

Table 3. Catch in numbers (millions) of Norwegian spring spawning herring in the adult fisheries 1950—1971.

Year class	Year							
	1950	1951	1952	1953	1954	1955	1956	1957
1930	3.6							
1931	0.9	0.5						
1932	18.5	8.7	3.8					
1933	42.4	18.4	28.1	22.2				
1934	171.9	158.0	127.7	95.4	63.2			
1935	107.0	119.5	83.2	89.6	80.0	43.0		
1936	66.4	47.4	65.3	73.8	89.2	72.6	45.0	
1937	368.3	348.0	256.3	233.9	247.4	104.6	75.7	31.3
1938	194.5	253.5	186.5	215.5	196.6	141.6	137.5	52.0
1939	86.9	107.6	106.8	98.8	126.8	115.2	122.8	61.8
1940	109.5	103.1	107.7	94.1	133.0	103.6	95.2	60.1
1941	88.6	82.7	85.7	91.2	100.6	84.6	88.9	42.5
1942	79.5	77.1	79.2	61.7	88.4	58.7	63.0	33.7
1943	628.6	602.0	377.9	394.9	460.7	203.2	163.3	131.6
1944	547.0	515.6	380.2	314.1	440.4	295.6	272.8	149.3
1945	185.5	164.4	204.5	110.9	199.8	193.4	198.3	121.2
1946	184.8	172.4	136.3	81.9	128.1	85.5	130.7	88.4
1947	276.2	383.8	602.3	355.6	490.3	274.7	264.2	182.5
1948		6.6	60.5	100.9	236.0	189.6	203.9	127.3
1949			39.3	46.6	142.9	114.3	110.0	72.0
1950				98.2	1 083.9	1 954.3	2 375.4	1 946.4
1951					55.8	262.2	275.8	220.5
1952						62.4	232.7	144.0
1953							27.9	246.1
1954								13.0
1955								
1956								
1957								
1958								
1959								
1960								
1961								
1962								
1963								
1964								
1965								
1966								
1967								
1968								
Total	3 160.1	3 169.3	2 931.1	2 579.3	4 363.1	4 358.8	4 883.1	3 723.7

Table 3 (cont.)

Year class	year						
	1958	1959	1960	1961	1962	1963	1964
1930							
1931							
1932							
1933							
1934							
1935							
1936							
1937							
1938	32.7						
1939	27.7	27.6					
1940	46.6	27.7	15.1				
1941	44.9	31.2	19.9	2.1			
1942	34.3	22.6	19.8	3.4	5.1		
1943	69.4	41.6	27.9	4.5	13.5	1.9	
1944	70.9	85.2	39.0	12.7	16.8	7.7	10.8
1945	77.4	77.4	47.2	15.7	30.3	19.3	14.3
1946	98.7	88.5	56.7	21.7	30.3	25.1	7.2
1947	200.9	198.0	153.5	63.0	79.2	61.8	46.6
1948	123.0	124.3	129.7	45.0	64.1	60.6	43.2
1949	70.7	88.6	85.2	49.7	49.3	79.8	46.1
1950	959.1	1 084.8	1 163.0	727.6	959.3	932.7	771.6
1951	192.9	239.7	203.9	136.1	138.9	174.1	151.9
1952	87.5	113.8	73.2	49.2	59.8	92.5	83.2
1953	100.3	138.0	93.8	61.5	64.1	107.7	96.3
1954	16.1	24.6	21.6	19.4	13.3	9.3	29.3
1955	8.0	22.8	23.3	14.9	20.2	18.3	24.9
1956		7.0	4.0	4.1	6.5	3.5	3.0
1957				1.8	2.0	1.7	1.5
1958					1.4	4.9	13.1
1959					255.7	408.9	1 917.7
1960					49.8	38.2	307.6
1961							90.2
1962							2.2
1963							
1964							
1965							
1966							
1967							
1968							
Total	2 261.1	2 443.4	2 176.8	1 232.4	1 859.6	2 048.0	3 660.7

Table 3 (cont.)

Year class	Year						
	1965	1966	1967	1968	1969	1970	1971
1930							
1931							
1932							
1933							
1934							
1935							
1936							
1937							
1938							
1939							
1940							
1941							
1942							
1943							
1944							
1945	4.3						
1946	8.7	5.5					
1947	21.7	16.5					
1948	52.1	8.8					
1949	70.2	14.9	1.9				
1950	703.0	392.7	64.3	5.4	1.1	0.2	
1951	137.7	96.9	14.3	4.1	0.2	—	
1952	106.9	72.1	14.3	3.6	0.3	0.1	0.02
1953	100.5	69.1	17.5	1.8	0.2	0.1	0.02
1954	40.0	11.0	8.9	2.6	—	0.1	0.02
1955	19.1	26.1	8.5	2.5	0.3	0.1	0.06
1956	7.4	17.4	3.5	0.8	0.2	0.1	—
1957	14.9	14.4	5.7	1.1	0.3	0.1	0.02
1958	19.5	38.0	8.9	2.0	—	0.1	—
1959	2 195.8	2 868.3	1 718.2	345.9	36.3	28.2	5.45
1960	570.4	1 290.6	1 135.0	134.8	33.5	26.7	6.91
1961	245.9	459.1	422.2	93.9	11.6	13.2	4.41
1962	12.1	26.1	27.0	14.3	0.7	1.0	0.36
1963	45.1	80.6	25.7	15.2	2.9	3.3	1.13
1964					—	0.4	1.01
1965					0.2	0.3	0.36
1966						1.3	0.94
1967						0.2	0.62
1968							0.32
Total	4 375.3	5 508.1	3 475.9	628.0	87.8	75.5	21.65

Table 4. Catch in numbers (millions) of Norwegian spawning spring herring in the young herring fisheries (small- and fat- herring) 1950–1974.

Year class	Year												
	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
1950	5 112.6	7 607.7	1 232.9	641.9	351.6	90.8	179.7	38.9	14.4	19.0	—	0.5	
1951		1 635.5	9 149.7	581.3	210.5	14.2	38.4	8.0	1.5	1.0	—	—	
1952			13 721.6	5 055.0	855.4	30.6	18.9	9.8	1.8	1.0	0.1	—	
1953				5 697.2	7 071.1	510.1	88.6	127.2	10.6	8.6	2.4	0.1	
1954					10 676.0	2 871.1	627.1	10.3	1.8	1.3	2.8	—	
1955						5 175.6	2 023.7	219.5	9.5	4.0	4.8	0.1	
1956							5 363.9	3 290.8	666.4	8.1	14.2	—	
1957								5 001.9	2 798.1	325.5	121.7	6.3	0.7
1958									9 667.0	1 985.3	392.5	31.2	6.6
1959										17 896.3	13 580.8	2 884.8	1 641.1
1960											12 884.3	16 075.6	1 006.5
1961												6 207.5	4 049.2
1962													3 687.5
Total	5 112.6	9 243.2	24 104.1	11 975.5	19 164.6	8 692.5	8 340.2	8 706.4	13 171.1	20 250.1	27 003.5	25 206.1	10 391.6

Year class	Year											
	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
1956	0.1											
1957	0.1											
1958	0.4	0.6										
1959	422.8	128.1	4.1	9.6								
1960	722.2	91.4	0.7	17.2								
1961	2 051.7	24.4	10.3	5.9								
1962	2 122.3	218.1	78.0	1.1								
1963	4 811.0	2 728.3	2 806.5	1 957.8	3 241,4	1 367,2	1,8					
1964		3 613.	3 752.0	1 671.0	1 395.5	1 900.6	8.9	2.9	0.1	0.5		
1965			2 303.0	664.0	70.3	98.8	0.6	0.3	—	0.2		
1966				3 893.0	9 911.1	385.4	188.1	17.3	0.3	1.0	0.1	
1967					428.0	435.3	142.2	6.4	0.4	2.2	0.4	
1968						1 782.0	507.9	33.5	1.5	1.6	0.1	
1969							555.9	530.1	85.1	33.6	10.9	5.3
1970								118.9	42.9	8.5	0.8	0.2
1971									30.5	52.3	0.3	0.1
1972										178.5	25.3	10.4
1973											18.0	23.1
1974												37.8
Total	10 130.5	6 803.9	8 954.5	8 219.0	15 046.3	5 969.2	1 405.3	709.4	160.8	278.4	56.0	77.0

Table 5. Spawning stock size in number (N × 10^{-9}) and weight (million metric tons) and fishing mortality 1950—1971. The figures in brackets are uncertain because of the information for the VPA being from only a few years catches.

Year	Spawning stock size		Fishing mortality			
	Number	Weight	4 years old	5 years old	6 years old	7 years old and older
1950	36.9	9.4	0.054	0.047	0.091	0.095
1951	30.3	9.1	0.050	0.062	0.051	0.12
1952	28.8	8.8	0.014	0.098	0.061	0.12
1953	23.5	7.1	0.016	0.028	0.074	0.14
1954	27.0	7.6	0.038	0.059	0.082	0.22
1955	34.1	8.8	0.051	0.067	0.058	0.17
1956	32.3	8.9	0.10	0.072	0.11	0.21
1957	35.8	10.0	0.17	0.079	0.066	0.13
1958	28.7	8.5	0.040	0.065	0.057	0.097
1959	23.3	7.5	0.074	0.072	0.110	0.13
1960	17.3	5.6	0.16	0.10	0.087	0.15
1961	13.1	4.2	0.089	0.048	0.068	0.11
1962	9.9	3.3	0.050	0.037	0.096	0.19
1963	7.5	1.6	0.057	0.041	0.030	0.29
1964	13.6	3.7	0.081	0.18	0.14	0.40
1965	17.8	4.5	0.17	0.15	0.29	0.75
1966	11.2	2.7	0.39	0.51	0.58	0.83
1967	4.8	1.3	1.1	0.80	1.2	1.5
1968	1.0	0.24	4.5	4.4	1.4	1.1
1969	(0.29)	(0.08)	(0.28)	(0.71)	(0.39)	(0.42)
1970	(0.17)	(0.06)	(1.31)	(0.34)	(0.60)	(0.63)
1971	(0.09)	(0.03)	(0.10)	(0.24)	(0.33)	0.3+

+ Assumed value.

RESULTS

ADULT STOCK

Table 5 shows the spawning stock size in number and weight and the fishing mortality on 4, 5, 6, 7 years old and older herring for the years 1950—1971, assuming a fishing mortality of 0.3 on the fully recruited year classes in 1971. A fishing mortality of 0.3 gives a spawning stock size of about 30 000 tonnes in 1971. The results of the calculations given in Table 5 are also plotted in Fig. 1 (stock size in number), Fig. 2 (stock size in weight) and Fig. 3 (fishing mortality on 7 years old and older herring).

The fishing mortalities are those generated by the total catch of an age group and not only the catch in the adult fisheries. It appears from Table 4 that some 4, 5 and 6 years old herring are also taken in the fat-herring

Fig. 1. Spawning stock size in number and total number of 4 years old and older herring (broken line) for the years 1950—1971.

Fig. 2. Spawning stock size in weight for the years 1950—1971. The broken line shows stock size estimates given by the Working Group on Atlanto-Scandian Herring (ANON. 1970, 1972).

fishery. The fishing mortalities on 4–6 years old herring have generally been lower than on 7 years old and older herring. The main reason for this is probably that these age groups show a more oceanic distribution throughout the year than do the older age groups. Thus, they have not been heavily exploited in the fat-herring fishery and have not been fully recruited to the adult stock. The extremely high fishing mortalities on 4 and 5 years old herring in 1968 (Table 5) were generated by the fat-herring fishery.

The spawning stock size was calculated by assuming full recruitment to

Fig. 3. Fishing mortality on 7 years old and older herring 1950—1968.

the adult stock at an age of 7 years. Portions of the younger year classes were added to the stock size of 7 years old and older herring given by the VPA. The quantity to be added for a year class of age t (t < 7) was calculated by:

$$N_t \text{ adult } = \frac{p_t}{p_{7+}} \cdot N_{7+}$$

where N_{7+} = total number of 7 years old and older herring.
p_t = percentage t years old herring in the winter fishery (Table 6).
p_{7+} = percentage 7 years old and older herring in the winter fishery.

The spawning stock size was at a level of about 9 million tonnes in 1950 (Table 5, Fig. 2) and decreased to about 7 million tonnes in 1953. From 1954 to 1957 the strong 1950 year class gradually recruited the spawning stock (Table 6), resulting in an increase in stock size which reached a peak of about 10 million tonnes in 1957 when the year class was fully recruited. The stock then decreased again as a result of poor recruitment, reaching a

minimum level of about 1.6 million tonnes in 1963. The fishing mortalities of the whole period 1950—1963 were on a low or moderate level (Table 5, Fig. 3).

The strong 1959 year class started to recruit to the spawning stock only to a small extent in 1963, but in 1964 it contributed about 60% to the spawning stock in number (Table 6).

The stock increased to about 3.7 million tonnes in 1964 and 4.5 million tonnes in 1965 (Fig. 2) when also the relatively strong 1960 year class recruited to the stock. From 1965 onwards there was a rapid decrease in spawning stock size due to an almost complete stop in recruitment to the adult stock and strongly increasing fishing mortalities. The last year class which recruited to the stock to any extent was that of 1961. The increase in fishing mortalities on the adult stock from 1964 onwards was primarily a

Table 6. Percentage age composition of Norwegian spring spawning herring during the Norwegian winter fishery 1950—1970.

Year Age	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
2	0.1	—	0.1	0.1	0.1	—	—	0.2	—	—	—	—	—
3	8.3	0.2	1.3	4.0	1.3	1.5	0.6	0.4	0.5	0.4	—	—	0.1
4	5.5	11.6	2.0	1.9	25.2	6.3	5.0	7.4	1.0	1.3	0.3	0.4	—
5	5.5	5.2	19.9	4.1	3.3	46.9	5.9	4.3	6.1	1.4	1.6	0.9	0.5
6	16.3	4.8	4.5	14.4	5.4	2.7	50.6	5.6	4.7	7.5	1.2	3.3	0.9
7	18.7	15.2	6.7	3.2	11.0	4.3	2.3	56.5	6.6	5.1	6.5	2.9	2.5
8	2.3	17.7	12.4	4.2	2.8	5.8	3.9	1.8	50.5	7.8	3.5	7.7	1.5
9	2.5	2.0	12.2	12.0	4.2	1.7	4.6	2.6	2.6	47.3	5.0	4.8	8.0
10	3.1	2.2	2.4	14.4	9.2	4.0	2.2	2.4	3.5	2.2	58.1	6.5	4.0
11	2.4	2.6	2.5	2.0	9.5	5.5	3.5	1.6	3.4	3.3	1.6	59.0	6.6
12	5.4	2.7	3.1	2.8	1.7	3.3	4.1	2.2	2.3	4.5	3.8	4.4	63.5
13	10.4	6.7	3.0	2.9	1.9	1.0	1.9	2.7	2.2	1.9	4.1	3.0	2.1
14	1.6	9.1	5.0	3.0	2.5	1.4	0.9	1.5	1.8	2.3	1.5	2.3	3.6
15	2.7	1.5	7.0	6.6	2.2	1.8	1.2	0.5	1.1	2.2	1.0	1.5	3.4
16	4.8	3.0	1.6	7.0	3.4	1.9	1.4	0.6	0.6	0.9	1.3	1.4	0.7
17	1.1	4.0	2.2	2.2	4.3	2.2	1.7	0.8	0.7	0.5	0.9	0.9	1.0
18	0.5	0.4	3.4	2.9	1.7	1.3	1.6	1.0	0.7	0.7	0.5	0.3	1.0
19	—	0.2	0.8	2.9	1.4	1.5	0.6	0.7	0.5	0.4	0.3	0.4	0.3
20	0.1	—	0.1	0.7	1.0	0.7	0.6	0.3	0.3	0.3	0.5	0.1	—
21	—	0.1	—	0.1	0.1	0.2	0.3	0.2	0.2	0.2	0.3	0.1	0.2
22	—	—	—	—	0.1	0.1	0.1	—	—	0.1	0.1	0.1	—
23	—	—	—	—	—	—	—	—	—	0.1	0.1	—	0.1
?	8.6	10.8	9.8	8.6	7.8	5.9	7.0	6.6	10.6	10.0	7.8	—	—
n	3 973	3 841	3 336	2 796	4 839	4 174	4 998	2 779	972	1 116	1 155	452	398

[1]) Age data from samples taken during experimental fishing.

Table 6 (cont.).

Year / Age	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972[1]	1973[1]	1974[1]
2	—	—	—	—	—	—	—	—	—	—	0.2	6.7
3	—	0.2	—	—	—	—	—	0.3	0.6	44.1	5.1	2.0
4	6.9	5.9	5.2	0.1	0.2	—	0.1	1.8	3.3	19.5	83.7	7.3
5	0.4	60.6	13.6	8.8	0.4	0.7	—	0.4	4.4	13.1	2.8	82.0
6	0.4	0.3	66.3	28.9	12.8	1.3	3.3	0.6	1.8	9.1	4.1	0.9
7	0.5	0.1	0.1	54.5	33.7	12.1	0.8	4.4	4.9	2.2	1.7	0.8
8	1.7	0.2	0.2	0.2	48.5	35.0	13.2	1.3	5.1	4.2	0.8	0.2
9	1.0	0.8	0.1	0.1	0.2	47.7	38.2	17.0	1.7	0.9	0.6	—
10	8.6	0.5	0.3	0.1	—	0.1	41.6	35.2	20.9	0.1	0.9	0.1
11	3.6	3.4	0.5	0.2	0.1	—	—	37.9	32.1	2.3	+	—
12	8.2	1.8	1.4	0.2	0.3	0.2	0.3	0.1	25.0	2.3	+	—
13	60.0	2.6	0.8	0.6	0.2	0.2	0.1	0.1	—	2.2	+	—
14	2.0	20.9	1.3	0.6	0.5	0.3	0.3	0.1	+	—	+	—
15	2.7	0.6	9.2	0.4	0.3	0.5	—	0.1	—	—	+	—
16	2.0	0.7	0.3	5.0	0.3	0.4	0.2	0.1	+	—	+	—
17	0.8	1.1	0.3	—	2.5	—	0.3	0.2	+	—	—	—
18	0.5	0.1	0.3	—	—	1.4	0.1	0.2	+	—	—	—
19	0.4	0.1	—	0.3	—	—	1.3	—	+	—	—	—
20	0.2	0.1	—	—	—	—	—	0.3	—	—	—	—
21	—	—	0.2	—	—	—	—	—	+	—	—	—
22	—	—	—	—	—	—	—	—	—	—	—	—
23	0.1	—	—	—	—	—	—	—	—	—	—	—
?	—	—	—	—	—	—	—	—	—	—	—	—
n	399	1 481	1 402	2 531	1 599	2 255	2 207	3 511	2 516	856	1 994	2 178

result of the escalation in the summer and autumn fishery off Iceland where the catch reached a peak about 1 million tonnes in 1966 (ANON. 1972).

The method used for estimating the spawning stock size is liable to errors in the age composition of the winter herring fishery, especially when strong year classes younger than 7 years old are present in the spawning stock. This was the case in the years 1954—1956 and 1963—1965.

After comparing the age composition of the winter herring fishery with the age composition of the total stock calculated by VPA, the estimates show that for the 1950 year class 16% of the 4 years old, 47% of the 5 years old, and 60% of the 6 years old fish spawned. For the 1959 year class the figures are 3%, 63% and 100% respectively.

There is an increasing trend in fishing mortality with age in the adult stock. This is illustrated in Fig. 4 where mean fishing mortalities of the age groups 7—9, 10—12 and 13—15 years are plotted for the period 1950—1965. In the period 1956—1965 the fishing mortality is consistently

Fig. 4. Mean fishing mortality on 7—9, 10—12 and 13—15 years old herring 1950—1965.

at a minimum for the age groups 7—9 and at a maximum for those of 13—15 years. The oldest age group used in the VPA is the 20 years old herring, and the difference illustrated in Fig. 4 can therefore hardly be explained by the fishing mortalities assumed for the oldest age groups used in the VPA.

There may be several explanations for the observed increase in the fishing mortalities with age.

Two possible explanations are indicated:

1) The exploitation rate on old herring may have been higher than on younger herring in the summer and autumn fishery as indicated by an observed difference in age composition between the winter fishery and the summer and autumn fishery, especially in the 1950s (FRIDRIKSSON 1963, DEVOLD 1963). It is interesting to note that the catches in the summer and autumn fishery show a significant increase around 1955,

Table 7. Fishing mortality by year class and age of young herring 1950—1969. The figures in brackets are uncertain because of the information for the VPA being from only a few years catches.

Age	Year class									
	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
0	0.058	0.07	0.75	0.35	1.12	0.92	0.73	0.80	1.38	0.30
1	0.11	0.64	0.66	0.91	1.06	1.18	1.45	1.59	1.27	0.37
2	0.023	0.07	0.21	0.14	0.67	0.34	1.52	0.78	0.91	0.12
3	0.016	0.04	0.03	0.04	0.04	0.04	0.10	0.73	0.15	0.10
Total	0.21	0.82	1.65	1.43	2.89	2.48	3.80	3.90	3.71	0.89

Table 7 (cont.)

Age	Year class									
	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969
0	0.35	0.45	0.79	0.22	0.26	1.17	0.28	0.46	1.32	0.50
1	0.92	0.58	1.62	0.18	0.44	1.38	2.63	1.18	2.36	(1.28)
2	0.12	0.62	0.69	0.28	0.34	0.47	0.93	1.96	(1.41)	(0.68)
3	0.12	0.06	0.65	0.31	0.50	3.26	1.98	(0.41)	(0.22)	(0.60)
Total	1.51	1.71	3.75	0.98	1.53	6.28	5.82	(4.01)	(5.31)	(3.06)

i. e. at the same time as the observed increase in fishing mortalities with age began.

2) Another possibility is that natural mortality increases with age. In the VPA the natural mortality is assumed constant; if, however, it increases with age, it will show up in the calculations as increasing fishing mortalities.

YOUNG HERRING

Table 7 shows the fishing mortality of the age groups 0—3 for the year classes 1950—1969, and Table 8 shows the year class size in number at different ages. The year class size of 0-group and 4 years old herring are plotted in Fig. 5.

The exploitation rate on young herring was high during the whole period of 1950—1969. From Fig. 5 and Table 8 it can be seen that there is clear correlation between year class size and survival during the young herring stages. The survival rate decreases with decreasing year class

Table 8. Stock size in numbers (N × 10⁻⁶) of young herring by year class and age and
survival (S) from 0-group to 4 years old 1950—1969. The figures in brackets are
uncertain because of the information for the VPA being from only a few years
catches.

Age	Year class									
	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
0	97 375	26 081	27 910	20 973	16 878	9 188	11 098	9 725	13 723	74 965
1	78 267	20 718	11 254	12 642	4 680	3 114	4 558	3 723	2 937	47 442
2	59 690	9 289	4 969	4 330	1 377	816	906	644	702	27 965
3	49 721	7 380	3 448	3 220	600	494	169	252	241	21 175
4	41 687	6 043	2 852	2 637	490	405	130	103	176	16 297
S	0.428	0.232	0.102	0.126	0.029	0.044	0.012	0.011	0.013	0.217

Table 8 (cont.).

Age	Year class									
	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969
0	47 478	18 327	7 242	26 264	17 305	3 560	17 334	1 245	2 587	1 515
1	28 631	9 927	2 807	17 957	11 426	942	11 194	669	589	(782)
2	9 751	4 754	475	12 792	6 297	201	682	175	(47)	(185)
3	7 337	2 175	203	8 281	3 832	107	230	(21)	(10)	(80)
4	5 552	1 747	91	5 185	1 987	4	(27)	(12)	(7)	(38)
S	0.117	0.095	0.013	0.197	0.115	0.001	(0.002)	(0.010)	(0.003)	(0.025)

strength. This is illustrated in Fig. 6 where the logarithm of the number
(ln N) is plotted against age for two weak year classes (1955 and 1962) and
two strong year classes (1950 and 1959). Year classes, recorded in the 1950s,
which traditionally have been called weak, were all, compared to the results
presented in Fig. 5, of what could be called an ordinary strength of 10 x 10⁹ –
30 x 10⁹ fish at the 0-group stage. However, year classes of strengths less
than 20 x 10⁹ as 0-group survived the fishery only in small quantities to
reach the age of 4 years. In addition to the year classes of ordinary strength
there were three extraordinarily strong year classes (those of 1950, 1959
and 1960). The 1965 year class (or possibly that of 1962) was the first one in
the period studied which really should ble classified as weak.

    The decreasing survival rate with year class strength indicates that the
same fishing effort in a purse seine fishery, such as that for young herring

Fig. 5. Year class strength in number as 0-group and 4 years old (broken line) 1950—1969.

going on in coastal waters, may generate a much higher fishing mortality when stock abundance is low than when the abundance is higher. However, it also reflects that strong year classes had a more offshore distribution, and that part of those year classes therefore were outside the traditional fishing areas (DRAGESUND and NAKKEN 1973).

The 1961 year class was the last one which recruited to the spawning stock in any quantity (Table 6). It can be seen from Fig. 5 and Table 8 that some herring of the relatively strong 1963 and 1964 year classes survived to an age of 4 years. The portions of these two year classes which survived the fishery during the first years of life were, however, practically fished out in the fat-herring fishery in 1968 going on off the Finnmark coast. The VPA for that year gives fishing mortality estimates as high as 4.5 (Table 5). The

Fig. 6. Logarithm of the number against age for selected year classes.

mortality of these two year classes at different ages is also illustrated in Fig. 6 where ln N is plotted against age.

At the 0-group stage the 1964 and 1966 year classes were of approximately the same strength (Table 8, Fig. 5). However, the 1966 year class was practically fished out in the small-herring fishery in 1967 which generated a fishing mortality of 2.6 in that year (Table 7). When the 1967–1969 year classes were at the 0-group stage, they were of the order of only 10% of the 1963, 1964 and 1966 year classes (Table 8), and the 1969 year class was the only one which was observed in the spawning stock in any quantities the years 1973—1975.

The VPA gives no reliable estimates of the strength of the 1970—1972 year classes, but they were all very weak, tentatively of the order of 10% of the 1967—1969 year classes, i. e. of the order of only 1% of the 1963, 1964 and 1966 year classes.

CONCLUDING REMARKS

The serious effect of the young herring fishery on the recruitment to the adult stock is clearly illustrated in Fig. 5. Even in the 1950s a year class apparently had to be of a size of about 20×10^9 in number as 0-group if a significant quantity was to have a chance to escape the small- and fat-herring fisheries. This means a year class strength of 2–3 times the average strength for the North Sea herring stock which has been estimated to be able to sustain an annual yield of about 800 thousand tonnes if properly managed (ANON. 1973). All year classes in the period 1950—1966, except those of 1962 and 1965, would probably have recruited the adult stock in at least the same quantity as the very strong 1960 year class did if they had not been fished as juveniles.

The 1963 and 1964 year classes were the last ones which survived to an age of 4 years in any quantity, but these two year classes were practically fished out in the fat-herring fishery in 1968 (Table 5, Fig. 6). DRAGESUND and ULLTANG (1972, 1973) discussed the possibility that increased natural mortality from 1968 onwards increased the rate of decline in the adult stock. The authors still regard this as a possibility, and it is also possible that some more fish of the 1963 and 1964 year classes, which never showed up in the spawning stock because of increased natural mortality, were left after 1968. Fishing mortalities of about 4.5, as estimated for these two year classes in 1968, mean that only 1% of the fish present at the beginning of the year survived the fishery, and this seems unlikely as the year classes in question had an offshore distribution in 1968.

The results of the present investigation leave, however, no doubt that the fishing pressure, especially on young and adolescent herring and also on adult herring in the years 1965—1968, was the primary factor for the

collapse of this herring stock. A possible increased natural mortality in later years may have been the result of the already extremely low stock size. In the same way as the fishing fleet was able to generate a much higher fishing mortality on weak than on strong year classes, as demonstrated in Fig. 6 and Table 7 and 8, the predators may have been able to generate a much higher natural mortality when the stock was so strongly depleted by the fishery.

It seems evident from Fig. 3 and 5 that the collapse could have been a reality at a much earlier stage if it had not been for the extraordinarily strong year classes of 1950, 1959 and 1960.

The weak year classes from 1967 onwards were probably the result of the low spawning stock size. If the decline in spawning stock size in 1967 reached the critical level where there is a clear relationship between spawning stock biomass and subsequent recruitment, it means that this critical level for the Norwegian spring spawning herring may be of the order of 1—2 million tonnes. The spawning stock size of 1967 was estimated to 1.3 million tonnes, or 0.8 when catch in the winter fishery is subtracted. The lowest level ever recorded earlier in the period studied, was 1.6 million tonnes in 1963, or 1.5 when catch in the winter fishery is subtracted, and the 1963 year class was relatively strong.

REFERENCES

ANON. 1951. *Annls biol., Copenh., 7* (1950): 122—125.
ANON. 1952. *Annls biol., Copenh., 8* (1951): 136—140.
ANON. 1953. *Annls biol., Copenh., 9* (1952): 164—167.
ANON. 1954. *Annls biol., Copenh., 10* (1953): 143—147.
ANON. 1956. *Annls biol., Copenh., 11* (1954): 114—118.
ANON. 1957. *Annls biol., Copenh., 12* (1955): 158—162.
ANON. 1958. *Annls biol., Copenh., 13* (1956): 173—176.
ANON. 1959. *Annls biol., Copenh., 14* (1957): 149—154.
ANON. 1960. *Annls biol., Copenh., 15* (1958): 126—131.
ANON. 1961. *Annls biol., Copenh., 16* (1959): 163—167.
ANON. 1962. *Annls biol., Copenh., 17* (1960): 161—166.
ANON. 1963 *Annls biol., Copenh., 18* (1961): 142—147.
ANON. 1970. Report of the working group on Atlanto-Scandian herring. *Int.Coun.Explor.Sea Coop.Res.Rep.Ser.A, 17*: 1—43.
ANON. 1973. Report of the North Sea Herring Assessment Working Group. *Coun.Meet.int.Coun.Explor.Sea, 1973* (H:27): 1—33. [Mimeo.]
ANON. 1974. Ressursoversikt for 1974. *Fisken og havet,* 1974 (særnummer): 1—102.
ANON. 1975 a. Ressursoversikt for 1975. *Fisken og havet,* (særnummer): 1—129.
ANON. 1975 b. Report of the working group on Atlanto-Scandian herring. *Coun.Meet.int.Coun.Explor.Sea, 1975* (H:4): 1—16. [Mimeo.]
ANON. 1976. Ressursoversikt for 1976. *Fisken og havet, 1976* (særnummer): 1—107.
BAKKEN, E. and DRAGESUND, O. 1971. Fluctuations of pelagic fish stocks in the northeast Atlantic and their technological and economic effects on the fisheries. *Organisation for Economic Co-operation and Development International Symposium on Fisheries Economics, Paris, 1971* (FI/T 1/6): 1—20, 7 fig. [Mimeo.]

337

DEVOLD, F. 1963. The life history of the Atlanto-Scandian herring. *Rapp. P.-v. Réun.Cons.perm.int.Explor.Mer, 154*: 98—108.

DEVOLD, F. 1968. The formation and the disappearance of a stock unit of Norwegian herring. *FiskDir.Skr.Ser.HavUnders., 15*: 1—15.

DRAGESUND, O. 1970. Distribution, abundance and mortality of young and adolescent Norwegian spring spawning herring *(Clupea harengus* Linne) in relation to subsequent year-class strength. *FiskDir.Skr.Ser.HavUnders., 15*: 451—556.

DRAGESUND, O. and ULLTANG, Ø. 1972. The collapse of the Norwegian spring spawning herring stock. *Coun.Meet.int.Coun.Explor.Sea, 1972* (H:11): 1—15. [Mimeo.]

DRAGESUND, O. and NAKKEN, O. 1973. Relationship of parent stock size and year-class strength in Norwegian spring spawning herring. *Rapp. P-v. Réun.Cons.perm.int.Explor.Mer, 164*: 15—29.

DRAGESUND, O. and ULLTANG, Ø. 1973. Further studies on stock size fluctuations and rate of exploitation of the Norwegian spring spawning herring, 1950—1971. *Coun.Meet.int.Coun.Explor.Sea, 1973.* (H:19): 1—13. [Mimeo.]

FRIDRIKSSON, A. 1963. Recent trends in the tribal composition of the north coast herring of Iceland. *Rapp. P.-v. Réun.Cons.perm.int.Explor.Mer, 154*: 68—72.

JAKOBSSON, J. 1963. Some remarks on the distribution and availability of the Iceland north coast herring. *Rapp. P.-v. Réun.Cons.perm.int.Explor.Mer, 154*: 73—82.

JAKOBSSON, J. 1968. Appendix. Herring migration east of Iceland during the summer and autumn 1966 and 1967. *FiskDir.Skr.Ser.HavUnders., 15*: 17—22.

ØSTVEDT, O. J. 1963. Catch, effort and composition of the Norwegian winter herring fishery. *Rapp. P.-v. Réun.Cons.perm.int.Explor.Mer, 154*: 109—117.

Received 30 May 1976
Printed 20 January 1978

SURVIVAL OF TAGGED BARENTS SEA CAPELIN (*MALLOTUS VILLOSUS* MÜLLER) AND ESTIMATES OF THE 1973, 1974 AND 1975 SPAWNING STOCKS FROM TAG RETURNS

By

ARE DOMMASNES

Institute of Marine Research, Bergen

ABSTRACT

DOMMASNES, A. 1978. Survival of tagged Barents Sea capelin *(Mallotus villosus,* Müller) and estimates of the 1973, 1974 and 1975 spawning stocks from tag returns. *FiskDir. Skr. Ser. HavUnders., 16* : 339—358.

Capelin tagged with internal stainless steel tags were kept in net enclosures for 8—9 days to obtain the survival factor. This was found to be 0.89 for males while additional information from routine tag recoveries indicated a survival factor of 0.51 for females.

The 1973 spawning stock was calculated separately from two different groups of tagged fish released at different times during the fishery. The resulting estimates were 2.2 and 4.1 million metric tonnes.

The 1974 spawning stock was calculated from three tagging experiments. The resulting estimates were 5.8, 1.1 and 1.9 million tonnes. The highest value is rejected as being obviously too high.

The 1975 spawning stock was calculated from two tagging experiments. Both gave an estimate of 1.1 million tonnes.

Some possible causes of error in the estimates are discussed.

INTRODUCTION

The Institute of Marine Research has carried out tagging of capelin with internal stainless steel tags since 1970, mostly during the winter fisheries on capelin migrating to the coast of Finnmark for spawning. The tags are recovered in fish meal factories by means of magnets in the production line and during cleaning of the machinery.

Tagging with internal metal tags and recovery by magnets was first described by ROUNSEFELL and DAHLGREN (1933). The method was later used successfully on herring (FRIDRIKSSON and AASEN 1950, 1952; AASEN 1958; DRAGESUND & HARALDSVIK 1966; ANON. 1975) and on mackerel (HAMRE 1975).

Abundance estimates of the 1971 and 1972 spawning stocks of Barents Sea capelin from tag returns have been published by DRAGESUND, GJØSÆTER and MONSTAD (1973).

Little knowledge is available on the survival of tagged capelin. DRAGESUND, GJØSÆTER and MONSTAD (1973) used 0.80 as an estimate of the survival factor for both females and males. Lack of information about survival has been one of the factors that seriously reduced the reliability of stock estimates based on tag returns. It was therefore decided to carry out a test experiment during the winter capelin fishery in 1974 to obtain more knowledge about the survival of tagged capelin.

THE SURVIVAL FACTOR

THEORY

The survival of tagged and untagged fish in the test can be expressed as follows:

$$S_1 = N_1 \cdot e^{-(M + T_1 + T_2 + L) \cdot t}$$

$$S_2 = N_2 \cdot e^{-(M + T_2) \cdot t}$$

or:

$$\frac{S_1}{S_2} = \frac{N_1}{N_2} \cdot e^{-(T_1 + L) \cdot t}$$

N_1 = number of tagged fish at the start of the test
N_2 = number of untagged fish at the start of the test
S_1 = number of tagged fish that survive without losing the tag
S_2 = number of untagged fish that survive
M = instantaneous natural mortality
T_1 = instantaneous mortality caused by the tagging operation
T_2 = instantaneous mortality caused by the handling apart from the tagging operation
L = instantaneous loss of tags (shedding)
t = time interval

Denoting $e^{-(T_1 + L) \cdot t}$ the tagging survival factor (s) we have:

$$s = \frac{S_1 \cdot N_2}{S_2 \cdot N_1} \tag{I}$$

The estimate of s obtained in this way includes the mortality caused by the tagging operation and the loss of tags up to time t. The estimate according to (II) is thus to be regarded as an overestimate, partly due to eventual limitation in t, and partly due to mortality caused by the handling apart from the tagging operation.

MATERIAL AND METHODS

The test was carried out in Nordvågen, approximately 7 kilometers east of Honningsvåg, in February and March 1974.

The capelin used in the experiments were caught by purse seine approximately 60 nautical miles off the coast. After capture the fish were transferred to two tanks (each approx. 1.5 m³) on the deck of the vessel. The tanks were continously supplied with seawater from a pump. Transport to the site of the experiment took 16 hours. The position of capture and of the test site are indicated in Fig. 3.

Tagging took place at the test site and was done according to the same procedure as in the open sea. The fish were taken one by one from the storage tanks with a dip net, and the tag was inserted by hand. No tagging gun, scalpel or other equipment was used, the tag being pressed into the body cavity without any sectioning in advance. This seems to cause the smallest wound. The tag was always inserted on the left side, slightly anterior to the anus (Fig. 1). After the tag had penetrated the body wall, it was turned so that it pointed straight forward, and then pushed completely into the abdominal cavity. Only fish larger than 15 cm were used. The tags, in lots of 50, were put into a jar of alcohol before use, and were picked out from there just before being inserted. As a result, both the tags and the fingers that came in contact with the wound were sterilized.

The tagged fish were collected in buckets and released into the net enclosures in batches of 10—25 fish.

The dimensions of the standard stainless steel capelin tags are 14 × 3 × 0.3 mm (Fig. 1).

The tagged fish and an equal number of untagged capelin were released into two net enclosures approximately 3.4 × 3.4 m at the surface and approximately 3.4 m deep. The surfaces of the enclosures were covered by nets. A 25 W electric lamp was placed in each enclosure to enable the fish to see the net wall. Into one enclosure 400 tagged and 400 untagged fish were released (Experiment 1), into the other 300 tagged and 300 untagged fish (Experiment 2). The surface temperature was 3.2°C where the fish were caught and 2.2°C at the experiment site.

Fig. 1. A capelin. The position where the tag is pushed into the abdomen is indicated by an arrow. A tag is shown in correct relative size.

Dead fish were scooped up with a dip net twice on the first day after the experiment started and every morning on the other days. The dead fish were examined for tags, measured, and sex and maturity were noted. All tagged fish had the position of the tag noted if still present. Loss of the tag was also noted. At the end of the test all remaining fish were scooped up, and the same information recorded. The sex was not noted before the fish were released into the enclosures.

RESULTS AND DISCUSSION

At the end of the test some fish were missing: in «Experiment 1» 29 tagged and 5 untagged fish; in «Experiment 2» 79 tagged and 77 untagged fish. There seem to be several reasons for the loss of fish. Some fish were taken by kittywakes *(Rissa tridactyla)* as they were released into the enclosures, before the cover net was in position. According to observers ashore others were taken by eider ducks *(Somateria mollissima)*. On two occasions corners of the cover net were torn loose by waves and wind so that it may have been possible for the ducks to dive into the enclosures. There were often large flocks of eider ducks around the test site. At the end of the test it was also found that one corner of the second enclosure («Experiment 2») where an anchor rope was fastened had been pulled under the surface by the current. At the same time the cover net had been pulled loose. This is probably the main reason why so many fish disappeared from «Experiment 2».

The three first series (50 fish in each series) of tagged fish in «Experiment 1» had very high mortality the first 20 hours. Most of them seemed to die immediately after release into the enclosure. This was probably due to lack of oxygen in the bucket where the fish were kept between tagging and release.

For the first three series about 25 fish were put into the bucket before they were transferred to the net enclosure. Later no more than 10 fish were collected in the bucket before transfer. For untagged fish the transfer probably did not create problems as it was much quicker for them. For all calculations except the tag retainment factor the three first series in «Experiment 1» have been disregarded. The remaining tagged fish in «Experiment 1», together with the 400 untagged fish in that enclosure, will be referred to as «Experiment 1a».

The results (Tables 1 and 2) show a very high mortality for both tagged and untagged females, much higher than for males. It is not possible from these results to calculate any reasonable value of the survival factor for females. The results give reason to suspect that for females the mortality from other factors than the tagging operation is so large that it obscures the tagging mortality.

Table 1. Results of Experiment 1a.

Experiment 1a	Date	Time	Tagged			Untagged		
			♀	♂	♀+♂	♀	♂	♀+♂
Released into net enclosures	20 Feb.	13.05—14.35	58[1]	192[1]	250	104[1]	296[1]	400
Recovered dead	21 Feb.	09.00	32	12	44	49	9	58
» »	21 »	16.00	5	4	9	10	5	15
» »	22 »	09.00	2	5	7	8	4	12
» »	23 »	09.15	7	2	9	11	7	18
» »	24 »	09.30	1	3	4	4	2	6
» »	25 »	09.30	2	1	3	2	2	4
» »	26 »	10.15	2	3	5	4	3	7
» »	27 »	09.10	0	2	2	6	12	18
» »	28 »	08.50	2	3	5	3	1	4
Total number of dead during experiment			53	35	88	97	45	142
Surviving fish recovered at end of experiment.......	28 Feb.	09.10	1	145	146	6	247	253
Total number of fish recovered			54	180	234	103	292	395
Total number of fish lost			4[1]	12[1]	16	1[1]	4[1]	5
Tag retainment factor[2]			––	0.95				
Surviving fish recovered retaining the tags[3]			––	145				

[1] The numbers have been estimated on the assumption that the sex ratio among fish released was the same as among those recovered.

[2] The tag retainment factor has been calculated from the complete «Experiment 1».

[3] This number has been calculated using the tag retainment factor.

Table 2. Results of Experiment 2.

Experiment 2	Date	Time	Tagged			Untagged		
			♀	♂	♀+♂	♀	♂	♀+♂
Released into net enclosures	20 Feb.	15.45—17.45	45[1]	255[1]	300	56[1]	244[1]	300
Recovered dead	21 Feb.	09.30	15	5	20	14	2	16
» »	21 »	16.00	3	6	9	11	1	12
» »	22 »	08.15	4	7	11	8	2	10
» »	23 »	09.00	3	2	5	4	3	7
» »	24 »	09.20	2	0	2	0	1	1
» »	25 »	09.00	2	4	6	2	2	4
» »	26 »	10.10	2	6	8	1	3	4
» »	27 »	09.00	1	5	6	1	3	4
» »	28 »	09.30	1	0	1	0	1	1
» »	1 March	08.30	0	4	4	0	2	2
Total number of dead during experiment			33	39	72	41	20	61
Surviving fish recovered at end of experiment	1 March		0	149	149	1	161	162
Total number of fish recovered			33	188	221	42	181	223
Total number of fish lost			12[1]	67[1]	79	14[1]	63[1]	77
Surviving fish recovered retaining the tags			0	145				
Tag retainment factor			--	0.97				

[1]) The numbers have been estimated on the assumption that the sex ratio among fish released was the same as among those recovered.

TAGGING SURVIVAL FACTOR FOR MALE CAPELIN, $s\male$.

In order to determine the numbers of each sex that were released into the net enclosures at the start of the experiment it was assumed that the sex ratio among the fish that were released was the same as for those recovered, and that mortality was the same among fish lost as among those recovered. The corresponding values of S_1, N_1, S_2 and N_2 are given in Table 3b, combination A. Using formula (I), «Experiment la» gives $s\male = 0.91$ and «Experiment 2» gives $s\male = 0.87$. The mean value is 0.89.

The most obvious sources of error in these estimates are the assumptions of the sex ratios of the fish originally released into the enclosures, and the theories of what happened to the lost fish. In Tables 3a and 3b are listed some other possible assumptions and the resulting values of S_1, N_1, S_2, N_2 and $s\male$. The lowest value of $s\male$, 0.85, is obtained from assumption E in «Experiment la». The highest value, 0.92, is obtained from several of the assumptions.

It is reasonable to assume that if all the fish that were released could have been accounted for, the test would still have given a value of $s\male$ somewhere between the above mentioned extremes. It is also probable that small variations in the handling and tagging technique, as are likely to occur if the tagging is done by different people, may cause the survival factor to change beyond the extremes calculated. This was demonstrated in the report from the ICES Working Group on the Bløden Tagging experiment 1969/70 (ANON. 1975) where two tagging teams were used, and it was found that the mean recapture rate of fish tagged by team 2 relative to team 1 was 0.73. It must be further remembered that $s\male$ only represents a maximum value for the tagging survival factor, because it does not take into account mortality due to stress from the catching procedure or the stay in the storage tanks.

Table 3a. Some possible combinations of sex ratio and mortality of the lost fish.

A   The sex ratios among the fish initially released into the enclosures was the same as among those recovered, and the ratio dead/survivors was the same among those lost as among those recovered in the groups «tagged» and «untagged», respectively.

B   The sex ratios among the fish initially released into the enclosures was the same as among those recovered, and all lost fish are considered as survivors.

C   The sex ratios among fish initially released into the enclosures was the same as among those recovered, and all lost fish are considered as dead.

D   All lost fish are considered as surviving males.

E   All lost fish are considered as dead males.

F   All lost fish are considered as females.

Table 3b. Values of S_1, N_1, S_2, N_2 and $s\sigma$ for the combinations of sex ratio and mortality given in Table 3a. Loss of tags has been included in s, using the «Tag retainment» factors given in Tables 1 and 2.

	Experiment 1a					Experiment 2				
	N_1	S_1	N_2	S_2	$s\sigma$	N_1	S_1	N_2	S_2	$s\sigma$
A	192	147	296	250	0.91	255	197	244	217	0.87
B	192	149	296	251	0.92	255	210	244	218	0.92
C	192	138	296	247	0.86	255	145	244	161	0.86
D	196	153	297	252	0.92	267	222	258	238	0.90
E	196	138	297	247	0.85	267	145	258	161	0.87
F	180	138	292	247	0.91	188	145	181	161	0.87

THE SIZES OF THE SPAWNING STOCKS

THEORY

When calculating the size of the capelin population based on tagging, the Petersen method was used (RICKER 1975):

$$(II) \qquad \hat{V} = \frac{C \cdot N \cdot s}{R} \qquad (II)$$

$\hat{V}$ = estimate of population at time of tagging,
C = size of catch after tagging in the same unit as $\hat{V}$,
N = number of fish tagged,
s = «tagging survival factor» which must also take into account loss of tags (shedding),
R = number of tags recovered.

When the sex of the tagged fish is known, the calculations are based on male fish only. If one assumes that the proportion of male capelin in the catches ($k\sigma$) is the same as in the spawning population, one can write:

$$\hat{V} \cdot k\sigma = \frac{C \cdot k\sigma \cdot N\sigma \cdot s\sigma}{R\sigma}$$

$$\hat{V} = \frac{C \cdot N\sigma \cdot s\sigma}{R\sigma} \qquad (III)$$

An estimate of the total spawning population ($\hat{P}$) disregarding natural mortality in the period concerned is found from the formula

$$\hat{P} = C_0 + \hat{V} \qquad (IV)$$

where C_0 is the catch taken before the tagged fish were released.

When the ratio $\frac{R}{C}$ is small, the standard deviation of the inverse value of V (RICKER 1975) is:

$$\text{St. dev.}\left(\frac{1}{V}\right) = \frac{\sqrt{R}}{C \cdot N \cdot s} \qquad\qquad\text{(V)}$$

Using (II) and (V) one obtains the 95% limits of confidence for $\left(\frac{1}{V}\right)$:

$$\frac{R - 1.96 \cdot \sqrt{R}}{C \cdot N \cdot s} < \frac{1}{V} < \frac{R + 1.96 \cdot \sqrt{R}}{C \cdot N \cdot s}$$

Inverting the values and introducing (IV) gives the 95% confidence limits for P:

$$C_o + \frac{C \cdot N \cdot s}{R + 1.96 \cdot \sqrt{R}} < P < C_o + \frac{C \cdot N \cdot s}{R - 1.96 \cdot \sqrt{R}} \qquad\qquad\text{(VI)}$$

or, adapted to (III):

$$C_o + \frac{C \cdot N\sigma \cdot s\sigma}{R\sigma + 1.96 \cdot \sqrt{R\sigma}} < P < C_o + \frac{C \cdot N\sigma \cdot s\sigma}{R\sigma - 1.96 \cdot \sqrt{R\sigma}} \qquad\qquad\text{(VII)}$$

MATERIAL AND METHODS

In order to calculate the spawning population the fish tagged in 1973 were divided into two groups, and calculations were made for each group separately. In 1974 three groups were used, in 1975 two groups.

In 1973 no attempt was made to determine the sex of the tagged fish, and the first 1000 fish tagged in 1974 were not sexed either. Later, each series of 50 tags was used for one sex only. The sex was determined from external characters.

The time of release for each group of tagged fish and the number of fish released is shown in Tables 4, 5 and 6 for 1973, 1974 and 1975, respectively. The areas of release are shown in Figs. 2, 3 and 4.

The input data used in the calculations were obtained as follows:

C_o was obtained from the catch statistics as the total catch fished before the date when the first tagged fish in the group were released. R and the corresponding C were obtained from plants that had a magnet efficiency coefficient above 0.40 in 1973, and above 0.50 in 1974 and 1975.

Table 4. Release dates and numbers of tagged capelin released in 1973.

	Date	Numbers released (Sex not determined)
	27 Feb.	1 500
Group 1	1 March	1 400
	2　»	1 000
	6　»	950
	8　»	150
Group 2	21　»	2 000
	22　»	1 500

Table 5. Release dates and numbers of tagged capelin released of each sex in 1974.

	Date	Numbers released		
		Sex not determined	♀	♂
Group 1	19 Feb.	1 000		
Group 2	11 March		1 000	1 000
	12　»		1 000	1 000
	13　»		1 000	1 000
	14　»		500	500
	15　»		500	500
Group 3	19 March		250	250
	20　»		900	600
	21　»		700	300
	25　»		1 000	500

Table 6. Release dates and numbers of tagged capelin released of each sex in 1975.

	Date	Numbers released	
		♀	♂
Group 1	8 March	500	1 000
	9　»		1 500
Group 2	15 March		2 000
	16　»		1 500
	17　»		1 000
	18　»		500

Fig. 2. Positions where tagged capelin were released in 1973.
1) Group 1, 2) Group 2.

The magnet efficiency coefficient, which is the proportion of retained tags to the number of tags in the catch produced, was determined by tagging in the usual way, but with unnumbered tags and «releasing» on the conveyor belt of the meal plant concerned. Of the 6 factories tested in 1973, 5 had magnet efficiency coefficients above 0.40. From one of these, however, no numbered tags were recovered and it too has been omitted from the calculations. In 1974, 12 factories were tested, and 7 had coefficients above 0.50. In 1975, 8 factories were tested, and 5 had coefficients above 0.50. The relevant values of R and the corresponding corrected catch C are shown in Tables 7, 8 and 9.

Where only tags from male capelin were used, the survival factor $s\,\sigma$ $=0.89$ was employed. For the 1973 material, where the sex of the tagged fish is not known, samples from the same area and time period indicate a sex ratio of 62% females to 38% males. Assuming a survival factor for females $s\,\varphi = 0.51$ (to be discussed later), a weighted value of $s = 0,65$ is obtained for the 1973 material. For group 1, 1974, samples indicate a sex ratio of 50 % females and 50% males, and a survival factor $s = 0.70$ has been used.

Fig. 3. Positions where tagged capelin were released in 1974.
　　　1) Group 1, 2) Group 2, 3) Group 3. The line indicates the transport of live capelin that were used in the tagging survival experiment.

RESULTS AND DISCUSSION
1973

Equations (II) and (IV) were used for calculation of the spawning population, and the 95% confidence interval was calculated from (VI). The input data used in the formulas are summarized in Table 10 and give the following results:

Group 1
Population estimate: $\hat{P} = 2.18 \times 10^6$ tonnes
Confidence interval: 1.93×10^6 tonnes $< P < 2.52 \times 10^6$ tonnes

Group 2
Population estimate: $\hat{P} = 4.12 \times 10^6$ tonnes
Confidence interval: 3.12×10^6 tonnes $< P < 6.54 \times 10^6$ tonnes

Table 7. Tag return efficiencies for the factories in 1973, quantities delivered to the factories after the tags were released (in metric tonnes), corrected quantities, returned tags and returned tags per 10 000 tonnes corrected quantity. Note that the designations A, B, C, ... do not cover the same factories each year.

Factory	Tag return effi- ciency	Group 1				Group 2			
		Quan- tity tonnes	Correc- ted quantity	Returned tags		Quan- tity tonnes	Correc- ted quantity	Returned tags	
				Total	per tonne $\times 10^4$			Total	per tonne $\times 10^4$
A	.95	30 008	28 508	42	15	12 247	11 635	5	4
B	.74	20 100	14 873	41	28	9 240	6 837	12	18
C	.48	72 290	34 698	48	14	22 543	10 820	3	3
D	.41	18 390	7 540	22	29	8 253	3 384	2	6
Total ...			85 619	153			32 677	22	

1974

For 1974 the spawning population was calculated from (II) and (IV) for Group 1 and from (III) and (IV) for Groups 2 and 3. The 95% confidence interval was calculated from (VI) for Group 1 and from (VII) for Groups 2 and 3. The input data are summarized in Table 11:

Group 1
Population estimate: $\hat{P}$ = 5.78 × 10⁶ tonnes
Confidence interval: 4.10 × 10⁶ tonnes $< P <$ 9.89 × 10⁶ tonnes

Group 2
Population estimate: $\hat{P}$ = 1.06 × 10⁶ tonnes
Confidence interval: 1.00 × 10⁶ tonnes $< P <$ 1.13 × 10⁶ tonnes

Group 3
Population estimate: $\hat{P}$ = 1.96 × 10⁶ tonnes
Confidence interval: 1.66 × 10⁶ tonnes $< P <$ 2.45 × 10⁶ tonnes

1975

For 1975 the spawning population was calculated from (III) and (IV) and the 95% confidence interval from (VII). The input data are summarized in Table 12:

Table 8. Tag return efficiencies for the factories in 1974, quantities delivered to the factories after the tags were released (in metric tonnes), corrected quantities, returned tags and returned tags per 10 000 tonnes corrected quantity. For Group 1 all tags returned from the factories in question have been used, for Groups 2 and 3 only tags from male fish. Note that the designations A, B, C, ... do not cover the same factories each year.

Factory	Tag return effi- ciency	Group 1				Group 2				Group 3			
		Quantity tonnes	Correc- ted quantity	Returned tags		Quantity tonnes	Correc- ted quantity	Returned tags		Quantity tonnes	Correc- ted quantity	Returned tags	
				Total	per tonne $\times 10^4$			Total	per tonne $\times 10^4$			Total	per tonne $\times 10^4$
A	.90	16 664	14 998	0	0	11 794	10 615	32	30	6 789	6 110	7	11
B	.81	21 625	17 516	2	1.1	16 218	13 137	50	38	7 079	5 734	5	9
C	.79	22 932	18 116	6	3.3	20 164	15 930	71	45	10 964	8 662	9	10
D	.78	95 807	74 729	3	0.4	53 801	41 965	172	41	27 166	21 189	22	10
E	.74	42 243	31 260	2	0.6	32 242	23 859	134	56	17 339	12 831	8	6
F	.61	21 081	12 859	5	3.9	17 086	10 422	52	49	7 658	4 671	6	13
G	.55	19 013	10 457	4	3.8	15 520	8 536	30	35	6 476	3 562	5	14
Total			179 935	22			124 464	540			62 759	62	

Fig. 4. Positions where tagged capelin were released in 1975.
        1) Group 1, 2) Group 2.

Group 1

Population estimate: $\hat{P}$ = 1.14 × 10⁶ tonnes

Population estimate: $\hat{P} = 1.14 \times 10^6$ tonnes

Confidence interval: 1.02×10^6 tonnes $< P < 1.29 \times 10^6$ tonnes

Group 2

Population estimate: $\hat{P} = 1.12 \times 10^6$ tonnes

Confidence interval: 1.04×10^6 tonnes $< P < 1.22 \times 10^6$ tonnes

A number of factors can have caused errors in the results. Some of these are discussed below.

The value used for the tagging survival factor is an obvious source of bias because it does not take into consideration the mortality caused by handling apart from the tagging operation. The actual tagging survival is therefore lower than indicated by s, and the population estimates given here must be regarded as overestimates.

A minimum requirement if a tagging experiment is to be used for calculating population sizes, is that the tagged fish must be randomly distributed in the population to be estimated or the fishing effort must be randomly distributed. If neither of these conditions is met, fishing mortality

Table 9. Tag return efficiencies for the factories in 1975, quantities delivered to the factories after the tags were released (in metric tonnes), corrected quantities, returned tags and returned tags per 10 000 tonnes corrected quantity. Only tags from male fish have been used. Note that the designations A, B, C, ... do not cover the same factories each year.

Factory	Tag return effi- ciency	Group 1				Group 2			
		Quan- tity tonnes	Correc- ted quantity	Returned tags		Quan- tity tonnes	Correc- ted quantity	Returned tags	
				Total	per tonne $\times 10^4$			Total	per tonne $\times 10^4$
A	.97	16 077	15 595	18	12	13 039	12 648	52	41
B	.78	10 076	7 849	12	15	9 358	7 299	100	137
C	.70	7 037	4 926	6	12	4 905	3 434	29	84
D	.69	69 385	47 876	143	30	47 237	32 594	128	39
E	.68	14 473	9 842	23	23	9 823	6 680	26	39
Total ...			86 098	202			62 655	335	

Table 10. Input data used to calculate the spawning stock in 1973.

	C_o (tonnes)	C (tonnes)	N	s	R
Group 1	362 033	85 619	5 000	.65	153
Group 2	739 426	32 677	3 500	.65	22

Table 11. Input data used to calculate the spawning stock in 1974.

	C_o (tonnes)	C (tonnes)	$N, N\sigma$	$s, s\sigma$	$R, R\sigma$
Group 1	58 433	179 935	1 000	.70	22
Group 2	238 495	124 464	4 000	.89	540
Group 3	469 246	62 759	1 650	.89	62

Table 12. Input data used to calculate the spawning stock in 1975.

	C_o (tonnes)	C (tonnes)	$N\sigma$	$s\sigma$	$R\sigma$
Group 1	190 609	86 098	2 500	.89	202
Group 2	283 672	62 655	5 000	.89	335

for the tagged fish is likely to be different from that of the whole population. In these experiments the tagged fish were released in batches in the areas where the fishing fleet was working. As a consequence, the first condition was probably not fulfilled. As to the second condition it is more difficult to say, but it was probably not fulfilled all the time.

The tag return efficiency was checked only once during the season for each factory. It is likely that efficiency is subject to some change during the season. This is indicated by the fact that there is considerable variation in the tag return efficiency for the same factory from year to year.

The two estimates for 1973 differ so much that their usefulness is seriously reduced, — 2.2 and 4.1 million tonnes, respectively. It is not possible from our material to tell whether the difference is due to one or more of the possible causes discussed above. It is therefore not really possible either to tell which of the two estimates is most correct. However, the lowest estimate is based on a higher number of released tagged fish and a larger catch. It therefore seems reasonable to put most emphasis on the lowest figure. On the other hand, an acoustic survey carried out in August 1972 resulted in an estimate of 3.7 million tonnes for the 1973 spawning stock (NAKKEN and DOMMASNES 1975). This is closer to the highest estimate from the tagging experiments.

In the case of Group 1 1974, fishing mortality for the tagged fish must have been much lower than for the rest of the population. Immediately after the tagging a storm blew up and stopped the fishing almost completely for more than a week. After the storm this concentration of capelin could not be relocated, and fishing started in another area. Observations (ANON. 1974) also indicate that the capelin tagged in Group 1 1974 may have had very high natural mortality due to predation from cod. The extraordinarily high population estimate resulting from the tags in Group 1 should therefore be disregarded.

Having decided to disregard the population estimate from Group I 1974, one is left with the estimates from Groups 2 and 3. Again the estimates differ rather a lot — 1.1 and 1.9 million tonnes, respectively. In this case it also seems most reasonable to accept the lower estimate as the best one. This agrees quite well with an acoustic survey in September–October 1973 which resulted in an estimate of 1.0 million tonnes for the 1974 spawning stock, with a possibility that the value might be as high as 1.5 million tonnes (NAKKEN and DOMMASNES 1975).

The estimates from Group 1 and Group 2 1975 both give a value of 1.1 million tonnes for the spawning stock. This does not exclude the possibility that both estimates may have been subject to error, but it still seems justifiable to put some confidence in the value. The acoustic survey in September–October 1974 resulted in an estimate of 0.8 million tonnes for the spawning stock in 1975 (NAKKEN and DOMMASNES 1975).

The widely differing estimates of the 1973 and 1974 stocks using different groups of tags and the possibilities of error pointed out in the discussion suggest that stock estimates for capelin based on tagging experiments should be used with caution. Even so, they are in the same size range as the acoustic estimates and are useful for checking those figures.

TAGGING SURVIVAL FACTOR FOR FEMALE CAPELIN, $s♀$.

For most of the capelin tagged in 1974 and all capelin tagged in 1975, each series of 50 tags was used for one sex only. It is thus possible to calculate the ratio between returned tags and released tagged fish separately for the sexes. If one assumes that fishing mortality is the same for both sexes, different values of this ratio must be due to mortalities from other causes than fishing. Of those other causes, natural mortality is likely to be small compared to tagging mortality so that any difference in the ratios between returned and released tags can be assigned to different tagging mortality alone:

$$\frac{R♀}{N♀ \cdot s♀} = \frac{R♂}{N♂ \cdot s♂}$$

$$s♀ = s♂ \cdot \frac{N♂ \cdot R♀}{N♀ \cdot R♂} \tag{VIII}$$

Table 13 shows the releases and recaptures by sexes for 1974 and 1975. Using these values and $s♂ = 0.89$ in equation (VIII) we get $s♀ = 0,51$ from the 1974 material and $s♀ = 0.59$ from the 1975 material. The 1975 sample is relatively small, and the 1974 estimate is therefore regarded as the most reliable one. Both samples confirm, however, the high tagging mortality for female capelin observed in the test experiments.

Table 13. Total numbers of capelin of each sex released in 1974 and 1975, and total numbers of tags returned.
$N♀, N♂$: numbers tagged
$R♀, R♂$: numbers of tage recovered.

Year	$N♀$	$N♂$	$R♀$	$R♂$
1974	6 850	5 650	644	931
1975	500	7 500	12	271

ACKNOWLEDGEMENTS

REFERENCES

AASEN, O. 1958. Estimation of the stock strength of the Norwegian herring. *J. Cons. perm. int. Explor. Mer, 24*(1): 95—110.

ANON 1974. Gyteinnsiget av lodde vinteren 1974. *Fiskets Gang, 60:*713–718.

ANON. 1975. Report of the ICES working group on the Bløden tagging experiment, 1969/70. *Int. Coun. Explor. Sea. Coop. Res. Rep., 1975* (47): 1—137.

BEVERTON, R. J. H. and HOLT, S. J. 1957. On the dynamics of exploited fish populations. *Fishery Invest., Lond. Ser. II 19*: 1—533.

DOMMASNES. A., NAKKEN, O., SÆTRE, R. and FRØILAND, Ø. 1974. Lodde- og polartorskundersø-kelser i Barentshavet i september—oktober 1973. *Fiskets Gang, 60*: 73—77.

DRAGESUND, O. and HARALDSVIK, S. 1966. Norwegian tagging experiments in the north-eastern North Sea and Skagerak, 1964 and 1965. *FiskDir. Skr. Ser. HavUnders., 14*: 98–120.

DRAGESUND, O., GJØSÆTER, J. and MONSTAD, T. 1973. Estimates of stock size and reproduction of the Barents Sea capelin in 1970–1972. *FiskDir. Skr. Ser. HavUnders., 16*:105–139.

FRIDRIKSSON, A. and AASEN, O. 1950. The Norwegian–Icelandic herring tagging experiments. Report no. 1. *FiskDir. Skr. Ser. HavUnders., 9*(11): 1—43.

FRIDRIKSSON, A. and AASEN, O. 1952. The Norwegian–Icelandic herring tagging experiments. Report No. 2. *Rit Fiskideild. 1952*(1): 1—54.

HAMRE, J. 1975. The effect of recent changes in the North Sea mackerel fishery on stock and yield. *Symposium on The Changes in the North Sea Fish Stocks and their Causes, Aarhus 1975* (22): 1–26, 15 tab., 6 fig. [Mimeo.].

NAKKEN, O. and DOMMASNES, A. 1975. The application of an echo integration system in investigations on the stock strength of the Barents Sea capelin *(Mallotus villosus* Müller) 1971—1974. *Coun. Meet. int. Coun. Explor. Sea, 1975* (B: 25): 1—9, 12 fig. [Mimeo.]

RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Bd Can., 191*: 1—382.

ROUNSEFELL, G. A. and DAHLGREN, E. H. 1933. Tagging experiments on the Pacific Herring, *Clupea pallasii. J. Cons. perm. int. Explor. Mer, 8*(3): 371—384.

DIFFERENTIATION BETWEEN «MARINUS» AND «MENTELLA» TYPES OF REDFISH BY ELECTROPHORESIS OF HAEMOGLOBINS

By

GUNNAR NÆVDAL

Institute of Marine Research, Bergen

ABSTRACT

NÆVDAL, G. 1978. Differentiation between «marinus» and «mentella» types of redfish by electorphoresis of haemoglobins. *FiskDir.Skr.Ser.HavUnders., 16* : 359–368.

Haemoglobins of 225 specimens of redfish from the Barents Sea and 357 specimens from Icelandic waters were analysed by electrophoresis to search for genetic differences between the morphologian *marinus* and *mentella* types. Two main haemoglobin patterns were commonly found, one characteristic for redfish of the *mentella* type and one characteristic for the *marinus* type. Specimens of *Sebastes viviparus* showed the *marinus* haemoglobin pattern. Morphological «intermediates» showed the *marinus* pattern in the Barents Sea while some specimens, which showed the *mentella* hemoglobin patterns, but could not be separated morphologically from the *marinus* type, were recorded in the Icelandic-Faeroe Ridge area. Four specimens showed a haemoglobin pattern which indicated hybridization between individuals with different haemoglobin pattern.

The results indicate that *Sebastes mentella* Travin is a species distinct form *Sebastes marinus* (L), possibly with occasional interbreeding. However, for final conclusion about the species of redfish in the North Atlantic samples have to be collected from the total range of the redfish's distribution.

INTRODUCTION

LUNDBECK (1940) claims that besides the common redfish, *Sebastes marinus* (L), a deep sea type excists in the Bear Island area and on the Iceland-Faeroe Ridge. TRAVIN (1951) described the deep sea redfish from the Bear Island area and the Barents Sea as a new species, *Sebastes mentella* Travin. This species prefers deeper water and somewhat higher temperature than *S. marinus* although they also occur sympatrically. *S. mentella* is characterized by a beak on its lower jaw, possesses a greater eye diameter, grows slower and reaches a smaller total length than *S. marinus*. The colour of *S. mentella* is bright red and of *S. marinus* usually orange-red.

ANDRIIACHEV (1954) and TEMPLEMAN (1959) restricted *Sebastes mentella* to the status of a subspecies, *S. marinus mentella,* because the differences between *marinus* and *mentella* were not clear enough to justify them as two

distinct species. TEMPLEMAN (1959) and others have found that *S. mentella* is not restricted to the Northeast Atlantic, but is common also in the Northwest Atlantic and occurred here in most localities in greater quantities than *S. marinus*.

By meristic, morphometric or morphologic methods clearcut separation of redfishes into *marinus* and *mentella* groups has been difficult (KOTTHAUS 1961, TEMPLEMAN 1959, KELLY, BAKER and CLARKE 1961). A great proportion of the specimens possessed the characteristics of both groups in a varying manner. However, genetical differences between the two groups were suggested by TEMPLEMAN and SANDEMAN (1959) who found great differences between *marinus* and *mentella* types in relative occurrence of caudal melanophores of pre extrusion larvae.

YANULOV (1962 a) found significant differences between the two types in infestation rate of various parasites in parts of the Northwest Atlantic.

By immuno-diffusion techniques, photron-reflectometric measurements and two separate methods of chromatography O'ROURKE (1961) found evidence for biochemical specificity of the two forms to such a degree that they could be considered as two distinct species. Similarly SCHAEFFER (1961) found that the two types differed significantly in content of certain free amino acids and total nitrogen content in muscle tissue.

In a series of papers (ALTUKHOV *et al.* 1968, ALTUKHOV and NEFYODOV 1968, ALTUKHOV, NEFYODOV and PAYUSOVA 1968, NEFYODOV 1969) dealing with the redfish problem, were described differences in muscle termostability and also differences in frequencies of some polymorphic serum proteins chartateristics (haptoglobins, albumins, and β-globulins) between samples of *marinus* and *mentella* types from the waters between Iceland and Greenland, showing tnat the analysed samples were not drawn from one homogenous population.

In the present paper differences in electrophoretic mobility of haemoglobins of the two types of redfish are described, and the results are discussed in relation to their significance on the systematic and the management of the redfish.

MATERIALS AND METHODS

Redfish for blood sampling was caught by bottom trawl. Blood was obtained by a syringe from the heart region, or the fish was cut open and blood collected into small glass tubes. After centrifugation the serum was pipettet off and the cells lysed by adding destilled water.

The haemoglobins were analysed by the agar gel electrophoresis at pH 7.2 describe by SICK (1965). Selected specimens were also analysed by the combined starch and agar gel electrophoresis at pH 9.0 described by MØLLER (1966). The haemoglobins were always analysed within 24 hours, usually

Table 1. Distributions of haemoglobin patterns in redfish from the Barents Sea and Icelandic
waters.

Sample no.	Locality	Date of sampling	Depth m	Mentalla-pattern	Marinus-pattern	Others	Sum
1	71°oo'N, 20° 00'E	7 November 1970	200	—	30	—	30
2	75°40'N, 16°50'E	10 » »	350	40	—	—	40
3	76°30'N, 13°50'E	12 » »	200	6	24	—	30
4	76°58'N, 12°30'E	12 » »	400	20	—	—	20
5	73°00'N, 33°45'E	17 » »	218	2	18	—	20
6	71°00'N, 34°42'E	19 » »	200	6	19	—	25
7	71°00'N, 29°06'E	19 » »	218	5	55	—	60
8	71°20'N, 26°40'E	20 » »	150	—	100	—	100
	Total, Barents Sea			79	246	—	325
9	64°20'N, 12°36'W	19 August 1971	236	9	27	2	38
10	63°20'N, 25°08'W	13 » »	300	—	158	2	160
11	65°38'N, 26°47'W	16 » »	280	3	156	—	159
	Total, Icelandic waters			12	341	4	357

within 12 hours from sampling. Parts of the material were reanalysed after
one or two days. Some haemoglobin specimens were also frozen and later
reanalysed at the Institute of Marine Research in Bergen. The haemoglo-
bins were stained by Amidoblack 10 B.

All samples from the Barents Sea were collected and analysed during a
cruise by R.V. «G. O. Sars» in November 1970 and the samples from
Icelandic waters likewise in August 1971. Fishing localities, depth, date of
sampling and number of specimens in each sample are listed in Table 1.
Fishing localities are also shown in Fig. 1 and 2.

All redfish specimen were separated morphologically into *Sebastes vivi-
parus* [backward directed anterior preopercular spine (ANDRIIASHEV 1954)],
mentella type, *marinus* type and intermediates [according to the description
by TRAVIN (1951)], and separation by morphology was compared to the
results from the haemoglobin analyses. Total length, usually also sex, were
recorded for the fishes of which blood was collected.

Fig. 1. Sampling localities of redfish in the Barents Sea.

<div style="text-align:center">RESULTS</div>

HAEMOGLOBIN TYPES OF REDFISH FROM THE BARENTS SEA

Among the samples from the Barents Sea were found two main haemoglobin patterns (Fig. 3). The first pattern occurred in specimens which according to TRAVIN (1951) were of the *mentella* type. In agar gel at pH 7.2 this pattern showed a strong, but rather diffuse anodic moving component, and one weak component stayed near the origin. By combined starch and agar gel electrophoresis at pH 9.0 the strong component showed high anodic mobility. Two weak components also showed anodic mobility while one very weak component moved slightly towards the cathode. This pattern was tentatively called the *mentella* pattern.

Fig. 2. Sampling localities of redfish in Icelandic waters.

The second pattern was found in specimens morphologically determined to be of the *marinus* type and consequently was called the *marinus* pattern. At pH 7.2 all components moved towards the cathode. Two weak components showed the highest mobility, and one strong component moved only slowly.

Individual variations were indicated in strength and occurrence of the two weak components, but this variation was not clear enough to form the basis of clearcut classification of the specimens. At pH 9.0 the strong component of the *marinus* pattern moved slower towards the anode than the strong component of the *mentella* pattern. Also in the *marinus* pattern was seen two weak components, one with intermediate anodic mobility and one with slight cathodic mobility.

One *Sebastes viviparus* from the Barents Sea (sample 1) showed the same haemoglobin patterns as individuals of the *marinus* type. Some specimens possessed morphological characteristics both of *marinus* and *mentella* types. This was especially evident at one locality on the Norwegian coast (sample 8) where the greater part of the specimens were recorded as such «intermediates» (SMESTAD, unpublished). However, with no exception all these specimens showed the *marinus* haemoglobin pattern.

Fig. 3. Outline of haemoglobin patterns in redfish obtained by gel electrophoresis. Filled in bars: Strong bands. Hatched bars: Moderately strong bands. Single lines. Faint bands. Arrow indicate the points of application.

The analysed specimens varied in length from about 15 to 40 cm, and both haemoglobin patterns were observed among the smaller as well as among the greater specimens. Consequently, no indications of ontogenetic variation in haemoglobin patterns were found in redfish.

The haemoglobin pattern could be recognized also after freezing and thawing of the hemolysate, but the clearest patterns were obtained with fresh material. No *post mortem* variation, except that the total patterns became diffuse, could be observed after proponged storage in the refrigerator.

The distribution of the two different patterns in the samples from the Barents Sea are shown in Table 1 (sample 1–8). The *mentella* pattern was found most frequently in the area between Bear Island and Spitsbergen and were rare in the eastern parts of the Barents Sea and near the Norwegian coast. Both were found together in the same trawl haul, but *mentella* occurred more frequently in deeper water. This is in accordance with the general appearence of the *mentella* type of redfish for instance from the description of Travin (1951).

Similar *mentella* and *marinus* haemoglobin patterns occurred among redfish samples from Icelandic waters as in the samples from the Barents Sea. In some specimens a modified *marinus* pattern occurred. This pattern showed an extra component which in agar gel at pH 7.2 moved slightly towards the anode and in combined starch and agar gel electrophoresis at pH 9.0 moved towards the anode with a mobility greater than the common strong component of the *mentella* pattern.

Totally 88 specimens of sample 10 and 19 specimens of sample 11, which were supposed to be *S. viviparus* from their backward directed preopercular spines, showed one of the two *marinus* patterns.

Few *mentella* patterns were found in Icelandic waters. West of northern Iceland (sample 11) were found three specimens out of 159 which showed the *mentella* pattern, and the fishes which possessed these patterns, were easily distinguished morphologically. West of Reykjanes (sample 10) were found no *mentella* patterns, and on Iceland-Faeroe Ridge (sample 9) were found 9 *mentella* patterns out of totally 38 specimens. In this sample all but one of the smaller fishes (9–13 cm) showed the *mentella* pattern, and also three fishes about 40 cm in length showed this pattern. However, in contrast to all other samples, morphological differentiation of the fishes showing the different haemoglobin types was nearly impossible, even for the greater specimens.

Four specimens, two in each of sample 9 and 10, showed a haemoglobin pattern with both the component of *mentella* and *marinus* pattern (Fig. 3). Morphologically these four specimens could not be distinguished from the *marinus* type, but because the pattern indicates hybridization between individuals with different haemoglobin types, this pattern tentatively was called the «hybrid» pattern. The fishes which showed this pattern ranged in length from 36 til 45 cm.

DISCUSSION

The compositions by amino acids of the proteins polypeptide chains and consequently the electrophoretic mobility of the proteins are controlled by genetic factors (MANWELL and BAKER 1970). The electrophoretic patterns of fish haemoglobins usually are species specific, illustrated by among others TSUYUKI *et al.* (1968) who described species specific electrophoretic patterns of haemoglobins of 28 species Pacific Ocean Scorpaenidae. Intraspecific variations of haemoglobin patterns, controlled by codominant alleles, have been described for several species (see de LIGNY 1969 for references). In other species, for example salmon (KOCH, BERGSTRØM and EVANS 1966) and herring (WILKINS and ILES 1966), intraspecific variations have been obser-

ved to be connected with ontogeny. Also variations due to changes in haemoglobin components after prolonged storage of samples have been described for several species, but these variations usually are found in the minor haemoglobin components (SICK 1965, MØLLER and NÆVDAL 1969, TSUYUKI *et al.* 1968, NÆVDAL 1968).

Neither ontogenetic cariation nor *post mortem* changes can account for the observed patterns of redfish haemoglobins because the two common patterns were observed in fishes ranging from less than 10 cm to more than 40 cm in length, all specimens were given the same treatment, and all were analysed within 24 hours from sampling. Control specimens did not show any major change in patterns even after two or three days in refrigerator or after freezing and thawing.

Segregation of two codominant alleles within one species could produce three patterns like the main patterns observed (the *mentella* and *marinus* patterns as homozygotes and the «hybrid» pattern as heterozygote). However, according to the Hardy-Weinberg law the hypothetical heterozygote (here the «hybrid» pattern) should then be expected to occur much more frequently than observed. It therefore seems unlikely that haemoglobin variation within one species can account for these patterns, but the modified *marinus* pattern in redfish from Icelandic waters may be normal intraspecific variation, probably genetically controlled.

However, the two common patterns may be explained by assuming that the *mentella* and *marinus* types of redfish really belong to different species, each with their own haemoglobin pattern. The «hybrid» pattern may be due to occasional hybridization between individuals of the two species. The good agreement, except in sample 9, between the results from the analyses of haemoglobins and morphological differenciation strongly support the theory of two species. Four hybrids out of more than 650 individuals do not show that the two types are conspecific because hybridization between related species is not uncommon among fishes. According to a second theory the «hybrid» pattern may represent an intraspecific variant of the *marinus* type. This theory is supported by the fact that the four specimens with the «hybrid» haemoglobin pattern could not be distinguished morphologically from the *marinus* type.

Although the *mentella* and *marinus* type of redfish seem to represent different species with only occasional interbreeding in the Barents Sea and Icelandic waters, the possibility still excist that the two types may be connected through intermediate populations in other areas. A definite conclusion about the species of redfish in the North Atlantic can therefore not be drawn until samples have been collected from the total geographic range of the redfish. However, the *marinus* and *mentella* types of redfish surely represent different *gene pools* with a minimum exchange of genetic material, and they therefore should be treated as separate units in management of the North-

east Atlantic fisheries. In addition, both the *mentella* and the *marinus* types may be composed of smaller units (populations, stock units) as claimed by SINDERMANN (1961) and YANULOV (1962 a, b) and others in their studies of parasites and meristic characteristics.

The fact that *Sebastes viviparus* showed the *marinus* haemoglobin pattern has no effect upon this conclusion. *Sebastes viviparus* doubtless is a true species (ANDRIIASHEV 1954, TROUT 1961), and two related species may have similar haemoglobin structure while others differ widely.

REFERENCES

ALTUKHOV, Ju., ARTEMJEVA, K. F., BORISOVA, I. V., and NEFYODOV, G. N. 1968. Immunological analysis of serum proteins of redfish in connection with maturation. *Res.Bull.int.Commn NW.Atlant.Fish., 5*: 44—48.

ALTUKHOV, Ju., NEFYODOV, G. N. and PAYUSOVA, A. N. 1968. Thermostability of isolated muscle in determining the taxonomic relationship of the *marinus-* and *mentella-*types of redfish *(Sebastes). Res.Bull.int.Commn NW.Atlant.Fish, 5*: 130—136.

ALTUKHOV, Ju. and NEFYODOV, G. N. 1968. A study of blood serum protein composition by agar-gel electrophoresis in types of redfish (genus *Sebastes). Res.Bull.int.Commn NW.Atlant.Fish., 5*: 86—90.

ANDRIIASHEV, A. P. 1954. Fishes of the northern seas the U.S.S.R. *Zool.Inst.Akad.Nauk SSSR, 53*: 1—566.

KELLY, G. F., BARKER, A. M. and CLARKE, G. M. 1961. Racial comparisons of redfish from the western North Atlantic and the Barent Sea. *Rapp.P.-v.Réun.Cons.perm.int.Explor.Mer., 150*: 28—41.

KOCH, H., BERGSTRØM, E., and EVANS, J. C. 1964. The microelectrophoretic separation on starch gel of the hemoglobins of *Salmo salar* L. *Meded.K.vlaam Acad., 26* (9): 1—32.

KOTTHAUS, A. 1961. Contributions to the race problem in redfish. *Rapp.P.-v.Réun.Cons.perm.int.Explor.Mer, 150*: 42—46.

LIGNY, W. de. 1969. Serological and biochemical studies on fish populations. *Oceanogr.Mar.Biol.Ann.Rev., 7*: 411—513.

LUNDBECK, J. 1940. Rotbarsch – Goldbarsch – Tiefenbarsch. *Dt.FischRdsch., 63* (2): 32—33.

MANWELL, C. and BAKER, C. M. A. 1970. *Molecular Biology and the Origin of Species: Heterosis, Protein Polymorphism and Animal Breeding.* Sidgwick and Jackson, London. 394 p.

MØLLER, D. 1966. Polymorphism of serum transferrin in cod. *FiskDir.Skr.Ser.HavUnders., 14*: 51—61.

MØLLER, D. and NÆVDAL, G. 1969. Studies om hemoglobin of some Gadoid fishes. *Fisk Dir.Skr.Ser.HavUnders., 15*:91–97.

NEFYODOV, G. N. 1969. Serum haptoglobins in the «marinus» and «mentella» types of North Atlantic redfish. *Int.Coun.Explor.Sea,Special Meet. The Biochemical and Serological Indentification of Fish Stocks, Dublin 1969* (29): 1—6.

NÆVDAL, G. 1968. Studies on hemoglobins and serum proteins in sprat from Norwegian waters. *FiskDir.Skr.Ser.HavUnders., 14*: 160—182.

O'ROURKE, F. J. 1961. An immunological and chromatographic study of *Sebastes marinus* (L) and *Sebastes mentella* Travin. *Rapp.P.-v.Réun.Cons.perm.int.Explor.Mer, 150*: 100—103.

SCHAEFFER, H. 1961. A biochemical contribution to the redfish problem. *Rapp.P.-v.Réun.Cons.perm.int.Explor.Mer, 150*: 104—110.

SICK, K. 1965. Haemoglobin polymorphism of cod in the Baltic and the Danish Belt Sea. *Hereditas, 54* : 19—48.

SINDERMANN, C. J. 1961. Parasitological tags for redfish of the western North Atlantic. *Rapp.P.-v.Réun.Cons.perm.int.Explor.Mer, 150*: 111—117.

TEMPLEMAN, W. 1959. Redfish distribution in the North Atlantic. *Bull.Fish.Res.Bd Can., 120*: 1—173.

TEMPLEMAN, W. and SANDEMAN, E. J. 1959. Variations in caudal pigmentation in late-stage pre-extrusion larvae from *marinus-* and *mentella-*type female redfish from the Newfoundland area. *J.Fish.Res.Bd Can., 16*: 763—789.

TRAVIN, V. I. 1951. En ny art av uer i Barentshavet *(Sebastes mentella* Travin sp.nov.) *Dokl.Akad.Nauk SSSR, 77* (4): 741—744. [Norwegian translation by Wiborg, K. F.]

TROUT, G. C. 1961. *Sebastes viviparus* (Krøyer) and the redfish problem. *Rapp.P.-v.Réun.Cons.perm.int.Explor.Mer, 150*: 94—99.

TSUYUKI, H., ROBERTS, E., LOWES, R. H., HADAWAY, W., and WESTRHEIM, S. J. 1968. Contribution of protein electrophoresis to rockfish (Scorpaenidae) systematics. *J.Fish.Res.Bd Can., 25*: 2477—2501.

WILKINS, N. P. and ILES, T. D. 1966. Haemoglobin polymorphism and its ontogeny in herring *(Clupea harengus)* and sprat *(Sprattus sprattus). Comp.Biochem.Physiol., 17*: 1141—1158.

YANULOV, K. P. 1962 a. Parasites as indicators of local rosefish stocks. P. 266—276 in MARTI, Ju. Ju. ed. *Soviet Fisheries Investigations in the Northwest Atlantic.* [English translation by Hershkowitz, B., Israel Program for Scientific Translations, Jerusalem 1963.]

YANULOV, K. P. 1962 b. On the groups of rosefish *(Sebastes mentella* Travin) in the Labrador-Newfoundland area. P. 277—289 in MARTI, Ju. Ju. ed. *Soviet Fisheries Investigations in the Northwest Atlantic.* [English translation by Hershkovitz, B., Israel Program for Scientific Translations, Jerusalem 1963.]