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THE EFFECT OF RECENT CHANGES IN THE NORTH SEA MACKEREL FISHERY ON STOCK AND YIELD

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INTRODUCTION

Mackerel, *Scomber scombrus* L., occur on both sides of the North Atlantic, restricted to the continental shelf regions. On the eastern side, mackerel occur from the Bay of Biscay to northern Norway. In this region two main spawning grounds have been defined, one in the North Sea and one in the Celtic Sea. In accordance with this, two major stocks probably exist in the region. One has its distribution centre in the central North Sea and the other in the area south of Ireland (Anon., 1974).

The present paper deals with aspects of the biology, stock structure, and exploitation of mackerel in the ICES statistical areas IIIa and IV, with special reference to the North Sea stock.

DISTRIBUTION AND MIGRATION

During spawning, which lasts from the end of May to the middle of July, mackerel disperse over a wide area in the Kattegat, the Skagerrak, and the North Sea. The centre of spawning is located in the central and southeastern North Sea (Iversen, 1973). After spawning, part of the stock migrates northwards and is found in the area around Shetland during July/August (Figure 171). Recent tagging experiments have shown a similar northward migration of post-spawners from the Celtic Sea.

In September/October the North Sea mackerel withdraw from the Kattegat, the Skagerrak, and the northern North Sea, and congregate in large concentrations on the Reef in the eastern North Sea. These large concentrations formed the basis for the very rich purse-seine fishery which developed in the mid-1960's. In late autumn the mackerel descend to deeper water in the northern part of the Norwegian Trench for wintering.

In April/May the mackerel return to the surface layer for feeding, and a migration towards the spawning grounds is reflected by the developing drift-net and hook-and-line surface fisheries. In April/May the

mackerel may still occur in schools dense enough for purse seining, but the schools disperse as the fish approach the spawning stage.

THE FISHERY

Prior to the early 1960's, mackerel were caught mainly by trawl, gillnet, and hook and line. A minor portion of the catch was taken by beach seine, and small Norwegian purse seiners operated in coastal waters. The total annual catch ranged between 66000 and 103000 tonnes (Table 75).

From 1964 on, the fishery grew rapidly owing to the development of the Norwegian purse-seine fishery, and reached a peak of 934000 tonnes in 1967. The catch decreased in the following years, and by 1970 it had fallen to 340000 tonnes. Since 1970 the Norwegian mackerel fishery has been regulated by a minimum legal size of 30 cm, closed seasons during winter and spring, and a catch-quota regulation of the autumn fishery. The bulk of the Norwegian purse-seine catch has been used for meal and oil, and the regulations apply to the industrial fishery only.

Figure 171 shows the main fishing grounds of the purse seiners by season. The peak season is September/October when the mackerel congregate on the Reef before they descend to deeper waters for wintering. Large catches were also landed from the area in May before the fish dispersed for spawning. The winter fishery in the Norwegian Trench fluctuated considerably according to the variation in the availability of the wintering schools, but on average it was of minor importance.

Owing to the restrictive measures affecting the industrial fishery in winter and spring, the purse-seine catch of pre-spawners has been negligible since 1970.

In 1969 the purse seiners started to fish mackerel in the area around Shetland, and this later became a regular fishery, with a season lasting from mid-July to the end of August. This fishery is based on two stock components, one from the North Sea, the other

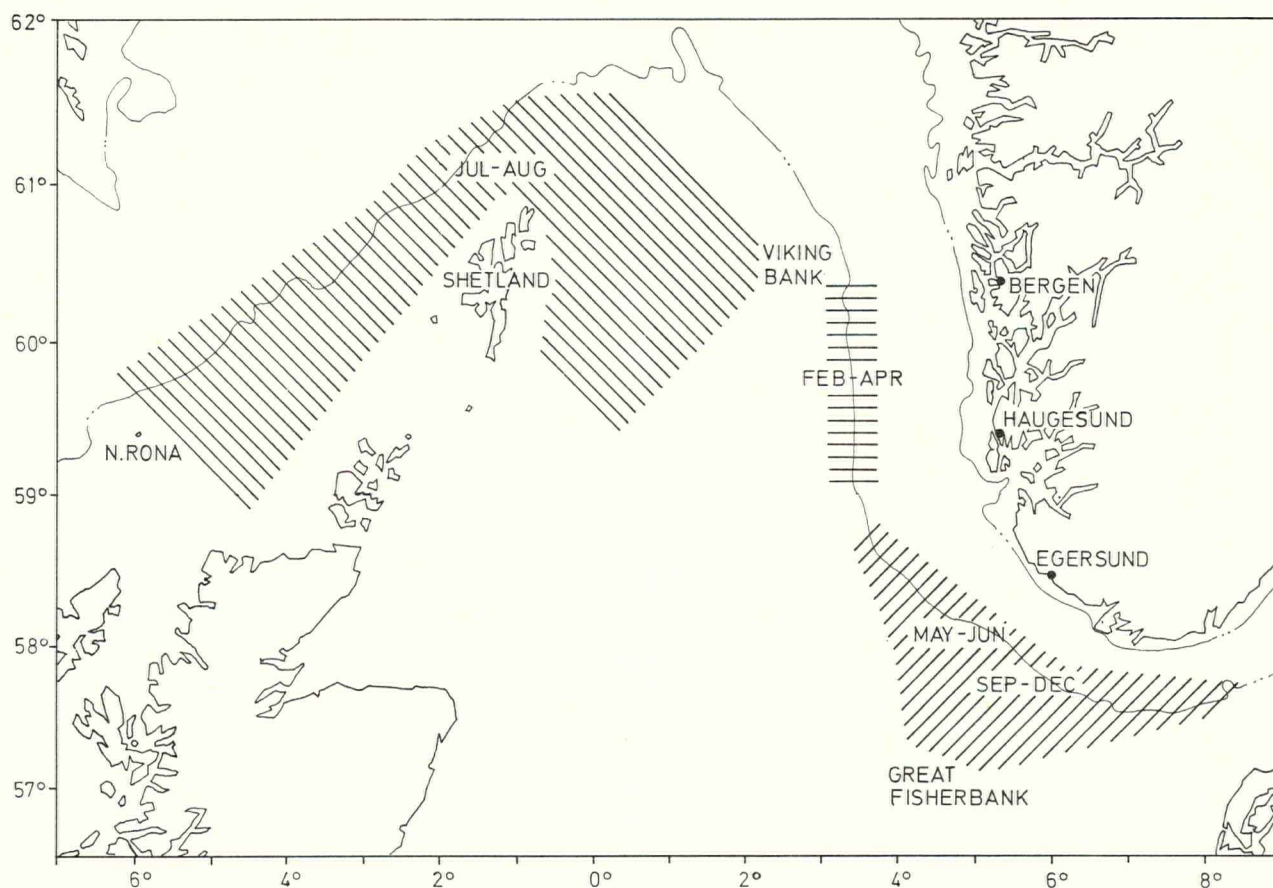


Figure 171. Main fishing grounds for Norwegian purse seiners by season.

from the western population, which spawn in the Celtic Sea area.

STOCK ASSESSMENT

Since 1969, the Institute of Marine Research has conducted a research programme for monitoring the state of the North Sea mackerel stock. The programme consists of annual releases of internally tagged fish and sampling of the commercial catches with respect to age composition and recoveries of tagged fish.

THE AGE COMPOSITION OF THE CATCH

Prior to 1970 the Norwegian mackerel catches were sampled randomly with respect to age composition. The catches used for reduction are paid for according to the fat content of the fish; therefore the landings are sampled individually for this purpose, and since 1969, length measurements have been obtained from these samples. The sampling programme covers the bulk of the Norwegian catch. In order to convert the lengths to age composition, samples for age-length

keys are drawn during the peak season. The catches from other gears are sampled randomly as in previous years. The age readings are based on otoliths, with the ages above 7 years grouped together owing to the low readability of otoliths in older age groups. The Norwegian mackerel catches by year class for the years 1970 to 1974 are shown in Tables 76-80. The time periods of the catches refer to the peak of the fishing season.

THE TAGGING PROGRAMME

Based on results from several test experiments on tagging methods carried out from 1965 to 1969, the present tagging programme was initiated in 1969 (Hamre, 1970). The programme consists of annual releases of internally tagged fish in July/August in the spawning area of the eastern North Sea and the Skagerrak. The fish are tagged from catches taken by trolling, and released continuously as the trolling vessel moves ahead with a speed of about 2 knots. The number released at various localities will thus be proportional to the hooking rate, which may tend to

Table 75. Total mackerel catch (tonnes) by country, 1964–1974, in the North Sea (IVa–c), the Skagerrak, and the Kattegat (IIIa). Data according to ICES Mackerel Working Group Report (Anon., 1975)

	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974 ^a
Belgium.....	125	138	67	201	77	139	19	85	129	78	?
Denmark.....	6 311	6 509	7 552	20 282	9 887	10 851	26 753	17 590	2 023	7 460	3 875
Faroe Islands.....	—	—	—	—	—	3 080	2 134	3 603	7 551	10 014	18 625
France.....	9 901	7 635	5 390	7 486	4 684	11 353	4 677	8 953	6 830	622	4 317
German Democratic Republic	—	—	—	—	—	—	—	—	—	—	233
Germany, Federal Republic of	3 495	2 221	1 501	2 132	1 353	1 161	225	408	374	563	?
Iceland.....	—	—	—	105	352	612	1 492	649	676	3 079	?
Netherlands.....	17 035	16 977	12 247	10 801	5 986	4 928	2 956	4 945	4 436	2 316	2 665
Norway.....	51 383	156 605	484 428	866 548	779 084	683 045	278 631	200 635	160 141	337 600	279 400
Poland.....	7 617	3 695	2 294	2 261	1 629	12	205	130	244	561	?
Sweden.....	15 006	13 364	13 754	15 246	11 783	10 820	4 407	3 157	4 748	2 960	?
U.K. (England and Wales) ..	67	76	99	46	55	35	35	23	32	30	35
U.K. (Scotland)	854	1 019	618	742	583	148	148	616	395	2 942	1 500
USSR.....	3 153	227	1 778	4 098	6 094	718	718	2 600	611	11 030	7 600
Total.....	114 997	208 466	529 728	929 948	821 567	726 902	322 400	243 394	188 190	379 255	318 250
Norway's part (%)	45	75	91	93	95	92	86	82	85	89	88

^a Provisional estimates.

ensure a proper mixing of the tagged fish in the population. The length of the tagged fish is measured, and samples of the catches are drawn regularly in order to establish age-length keys.

The tags are recovered on magnets installed in the machinery of the reduction plants. The efficiency of the magnets is tested each year, and the recoveries and corresponding production are reported regularly by the plants on standard forms.

DATA COMPILATION

The programme yields recovery data from successive releases, with a time period of one year between releases. The data from such a programme may be set out in a triangular array as in Table 81. In the

table, m is the number released, and r is the number recovered in the sample or catch. The index i denotes the successive time intervals of releases and j those of recoveries; s is the factor which compensates for the mortality $(1 - s)$ caused by the tagging operation.

From such an array various estimates of annual survival S may be obtained:

$$S_i = \frac{s_{i+1} \ m_{i+1} \ r_i, (j = i+1)}{s_i \ m_i \ r_{(i+1)}, (j = i+1)} \quad (\text{Ricker, 1945}) \quad (1)$$

$$S_i = \frac{s_{i+1} \ m_{i+1} \ r_i, (j = i+2)}{s_i \ m_i \ r_{(i+1)}, (j = i+2)} \quad (\text{Bailey, 1951}) \quad (2)$$

The estimate (2) excludes all within-season recaptures. This may avoid error due to incomplete

Table 76. Norwegian mackerel catches (N in millions of individuals) by gear, area, and year class in 1970 and autumn 1969

Year class	North Sea 1970								Shetland 1970		North Sea 1969	
	Gillnet Apr-Jun		Hook and line Jul-Sep		Purse seine Sep-Oct		Total	Purse seine Jul-Aug		Total 1970	Sep-Dec	
	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	<i>N</i>	%	<i>N</i>	<i>N</i>	%
1969.....			0.915	7.3	66.717	15.7	67.632			67.632		
1968.....	1.197	12.1	5.677	45.2	107.042	25.2	113.916	8.825	5.7	122.741	21.805	3.8
1967.....	0.821	8.3	1.577	12.6	42.765	10.0	45.163	8.306	5.4	53.469	41.187	6.5
1966.....	2.130	21.4	2.681	21.4	103.774	24.4	108.585	28.033	18.1	136.618	174.440	27.9
1965.....	1.450	14.6	0.757	6.0	36.245	8.5	38.452	31.148	20.1	69.600	113.871	18.2
1964.....	0.335	3.4	0.252	2.0	10.733	2.5	11.320	15.055	9.7	26.375	29.073	4.7
1963.....	0.243	2.4	—	—	2.832	0.7	3.075	11.421	7.4	14.496	13.325	2.1
Older.....	3.752	37.8	0.694	5.5	55.192	13.0	59.638	51.913	33.6	111.551	230.165	36.8
Σ <i>N</i>	9.928		12.553		425.300		447.781	154.701		602.482	623.866	
Tonnes	5.018		5.015		185.420		195.453	89.042		284.495	314.005	

Table 77. Norwegian mackerel catches (N in millions of individuals) by gear, area, and year class in 1971

Year class	North Sea						Shetland	
	Gillnet		Hook and line		Purse seine	Total	Purse seine	Total
	Apr-Jun		Jul-Sep		Sep-Oct		Jul-Aug	
	N	%	N	%	N	%	N	%
1970.....					0.700	0.9		0.700
1969.....	2.659	20.8	14.763	71.6	57.657	74.1	13.366	4.2
1968.....	2.351	18.4	1.897	9.2	7.416	9.5	28.390	9.0
1967.....	1.015	7.9	0.718	3.5	2.679	3.4	35.550	11.2
1966.....	2.685	21.0	1.282	6.2	4.358	5.6	78.420	24.8
1965.....	1.028	8.1	0.410	2.0	1.992	2.6	77.608	24.5
1964.....	0.514	4.0	0.359	1.8	0.283	0.4	15.898	5.0
Older.....	2.531	19.8	1.179	5.7	2.728	3.5	67.479	21.3
ΣN	12.783		20.608		77.813		316.711	
Tonnes	5.621		6.669		23.793		166.557	

Table 78. Norwegian mackerel catches (N in millions of individuals) by gear, area, and year class in 1972

Year class	North Sea						Shetland	
	Gillnet		Hook and line		Purse seine	Total	Purse seine	Total
	Apr-Jun		Jul-Sep		Sep-Oct		Jul-Aug	
	N	%	N	%	N	%	N	%
1971.....					0.087	0.1		0.087
1970.....			0.305	1.6	1.987	1.4	1.752	0.9
1969.....	1.194	10.4	14.741	76.7	90.772	64.8	41.844	21.9
1968.....	1.524	12.7	1.272	6.6	14.858	10.6	26.732	14.0
1967.....	1.194	10.4	0.697	3.6	9.539	6.8	23.116	12.1
1966.....	1.958	15.8	1.251	6.5	10.483	7.5	25.129	13.2
1965.....	1.119	9.0	0.099	0.5	10.925	7.8	28.094	14.7
Older.....	5.176	41.7	0.861	4.5	1.445	1.0	44.211	23.2
ΣN	12.215		19.226		140.096		190.878	
Tonnes	6.135		6.787		51.358		91.706	

Table 79. Norwegian mackerel catches (N in millions of individuals) by gear, area, and year class in 1973

Year class	North Sea						Shetland	
	Gillnet		Hook and line		Purse seine	Total	Purse seine	Total
	Apr-Jun		Jul-Sep		Sep-Oct		Jul-Aug	
	N	%	N	%	N	%	N	%
1972.....					1.608	0.5		1.608
1971.....			0.458	3.5	7.153	2.4	0.339	0.1
1970.....	0.087	1.0	0.915	7.1	16.619	5.5	15.200	3.9
1969.....	4.190	49.8	8.236	63.5	182.183	60.6	74.564	19.4
1968.....	1.284	15.2	1.732	13.4	40.761	13.6	74.366	19.4
1967.....	0.359	4.2	0.392	3.0	19.791	6.6	29.431	7.7
1966.....	1.045	12.4	0.392	3.0	10.722	3.6	49.969	13.0
Older.....	1.447	17.2	0.850	6.5	21.505	7.2	140.078	36.5
ΣN	8.412		12.975		300.342		383.947	
Tonnes	3.893		5.130		127.183		201.394	

Table 80. Norwegian mackerel catches (N in millions of individuals) by gear, area, and year class in 1974 (revised figures)

Year class	North Sea							Shetland				
	Gillnet		Hook and line		Purse seine		Total	Purse seine		Total		
	Apr-Jun		Jul-Sep		Sep-Oct			Jul-Aug		Nov-Dec		
	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	<i>N</i>	%	<i>N</i>	%	<i>N</i>
1973.....			0.115	2.5	0.886	0.6	1.001	0.243	0.1	0.908	0.9	2.152
1972.....	0.476	7.0	0.160	3.6	8.241	5.4	8.877	1.245	0.3	4.903	5.0	15.025
1971.....	0.020	0.3	0.160	3.6	11.962	7.9	12.142	15.212	4.2	3.813	3.9	31.167
1970.....	0.248	3.7	0.252	5.6	17.692	11.6	18.192	27.662	7.5	9.297	9.4	55.151
1969.....	3.593	53.0	2.634	59.2	87.468	57.6	93.695	126.678	34.8	64.242	65.0	284.615
1968.....	0.715	10.5	0.275	6.1	12.046	7.9	13.036	47.428	13.0	7.009	7.1	67.473
1967.....	0.258	3.8	0.069	1.5	2.027	1.3	2.354	25.870	7.1	2.687	2.7	30.911
Older.....	1.469	21.7	0.779	17.5	11.774	7.7	14.022	119.725	32.9	5.919	6.0	139.666
Σ <i>N</i>	6.779		4.444		152.096		163.319	364.063		98.778		626.160
Tonnes	3.579		2.065		66.313		71.957	174.660		41.126		287.743

mixing of the tagged fish. If the tagged fish are randomly mixed, the fraction $r_{ij}/r_{(i+1)j}$ is a random variate with respect to the sampling period j . A weighted estimate of S corresponding to Equation (1) can thus be obtained:

$$S_i = \frac{s_{i+1} m_{i+1} \sum_{j=i+1}^j r_{ij}}{s_i m_i \sum_{j=i+1}^j r_{(i+1)j}} \quad (3)$$

Summing r_{ij} from $j = i + 2$ to j , all within-season recoveries in Equation (3) are excluded.

The estimate of S does not include the catch, and is consequently not influenced by the error which is introduced when recaptured tags are not reported. The estimate does include the mortality caused by tagging, but if the variation in s is small, the fraction s_{i+1}/s_i approaches unity. Standardizing the field work is therefore of particular importance for the accuracy of the estimate.

Table 81. Triangular array of recovery data from successive releases; m = number released, r = number recovered, and s = survival factor. The indices i and j denote successive intervals of releases and recoveries respectively

$i \ j =$	0	1	2	3	4	j	
$s_0 \cdot m_0$	0	r_{00}	r_{01}	r_{02}	r_{03}	r_{04}	r_{0j}
$s_1 \cdot m_1$	1		r_{11}	r_{12}	r_{13}	r_{14}	r_{1j}
$s_2 \cdot m_2$	2			r_{22}	r_{23}	r_{24}	r_{2j}
$s_3 \cdot m_3$	3				r_{33}	r_{34}	r_{3j}
$s_4 \cdot m_4$	4					r_{44}	r_{4j}
$s_i \cdot m_i$	i						r_{ij}
Catch:	C_0	C_1	C_2	C_3	C_4		C_j

In estimating the recruitment R , the following formula is used:

$$R_j = \frac{e_{j+1} C_{j+1} \sum_{i=0}^{i=j} r_{ij}}{e_j C_j \sum_{i=0}^{i=j} r_{(j+1)i}} \quad (4)$$

where e is the coefficient of magnet efficiency. Summing r_{ij} from $i = 0$ to $i = j - 1$, the within-season recaptures in Equation (4) are excluded.

The formula (4) provides an estimate of the recruitment for the period between sampling and is independent of any systematical error in the magnet efficiency tests.

Summing the array vertically, the sum $\sum_{i=0}^{i=j} r_{ij}$ is the total number of recoveries in the sample drawn in time j . Assuming a constant s , a single census estimate of the stock size N at time j may be formulated as:

$$N_j = \frac{C_j s \sum_{i=0}^{i=j} m_{ij}}{\sum_{i=0}^{i=j} r_{ij}} \quad (5)$$

where C_j is the catch in number, and $\sum_{i=0}^{i=j} m_{ij}$ is the total number of surviving tagged fish at the beginning of the sampling period j , including all the previous releases.

An estimate of the number of surviving tagged fish at any time interval prior to j is obtainable according to the formula (3), provided that the total mortality rate measured between the releases in the interval i to $i + 1$ is valid for all the previous releases. This assumption is basically the same as the general assumption on which the use of tagging data is founded,

namely that the tagged fish after having recovered from the tagging operation are subject to the same mortality rate as the population under study.

In mathematical terms, the number of surviving tagged fish from the release m_i at the time of sampling j can thus be written:

$$m_{ij} = m_i S_i S_{i+1} S_{i+2} \dots S_{i+(j-1)}$$

and the total m_{ij} at time j :

$$\sum_{i=0}^{i=j} m_{ij} = \sum_{i=0}^{i=j} m_i S_i S_{i+1} S_{i+2} \dots S_{i+(j-1)} \quad (6)$$

where S is estimated according to Equation (3). The within-season recaptures may be excluded in Equation (5) by summing from $i = 0$ to $(j - 1)$. In principle the stock estimate given in Equation (5) is the same as that used by Fisher and Ford (1947) in their study of an insect population.

The mortality caused in the tagging operation, $1 - s$, has been studied on the basis of a test experiment in which tagged and untagged fish were kept under observation over a certain period. The test indicates a mortality caused by the implantation of the tag of about 10 % (Hamre, 1970). The magnitude of s , including the deaths caused by the catching method and the handling of the fish prior to the tagging, has been studied on the basis of catch statistics and estimated mortality.

The method used in this respect is founded on the basic formula of cohort analysis:

$$\frac{N_{t+1}}{C_t} = \frac{\exp(-z)}{E[1 - \exp(-z)]}$$

where N is the stock size, C the total catch, z the total instantaneous mortality coefficient, and $E = F/(F + M)$ the rate of exploitation. Applying the time indices used above, the formula may be written ($i = j$):

$$N_{i+1} = \frac{C_j \exp(-z_i)}{E_i[1 - \exp(-z_i)]} = sN'_{i+1}$$

or

$$s = \frac{C_j}{N'_{i+1}} \frac{\exp(-z_i)}{E_i[1 - \exp(-z_i)]} \quad (7)$$

where N'_{i+1} is the estimated stock size based on Equation (5) disregarding the mortality caused by the tagging.

In Equation (7) there are two unknown parameters, s and M , the natural mortality rate. Regarding both as constant, two sets of data fitted into the formula are thus sufficient to derive estimates of s and M if the two data sets represent different levels of fishing mortality.

It has been observed that the number of tag returns per unit of catch is significantly lower in the catches from the Shetland area than in those from other parts of the North Sea. This observation would indicate that the fishery in the Shetland area is partly based on another stock. This has subsequently been confirmed by recoveries of tagged fish released in the Celtic Sea.

The annual releases in the North Sea form a basis for a closer study of this observation. The problems involved are basically of the same nature as those of the recruitment study. Providing that tagged and untagged fish migrate into the Shetland area in the same proportion as observed in the previous autumn catches of the North Sea, the following equation is obtained:

$$p_j = \frac{(P_j)_N}{(P_j)_S} \frac{\left(\sum_{i=0}^{i=j-1} r_{ij} \right)_S}{\left(\sum_{i=0}^{i=j-1} r_{ij} \right)_N} \quad (8)$$

where p is the proportion of the Shetland catch originating from the North Sea stock, assuming the year classes concerned to be fully recruited to the catchable stock. Here $(P)_N$ denotes the quantity of the North Sea catch used for production of fish meal from which the recoveries $(\sum r_i)_N$ have been reported; $(P)_S$ and $(\sum r_i)_S$ are the corresponding figures of the Shetland fishery. As for the recruitment formula, the recoveries of all liberations may be summarized when inserted in Equation (8), but in order to avoid error due to incomplete mixing, all within-season recaptures are in this case excluded.

ESTIMATES OF SURVIVAL AND RECRUITMENT

Owing to various circumstances it is convenient to arrange the tagging data in two groups of ages, one containing the 1969 year class, the other including the older year classes.

Table 82 summarizes the releases m , recoveries r , and corresponding fish production (P in millions of individuals) in the years from 1970 to 1974 for the 1969 year class. Recaptures from the autumn fishery in the eastern North Sea and those reported from the Shetland fishery in summer are grouped separately (columns marked NS and Sh, respectively). The time intervals ij run from September to August, with i referring to the time of release (September), j to the time of recapture (September–August).

The survival S_i is calculated according to Equation (3) and measures the difference in survival of tagged fish from two successive releases, assuming that the mortality caused by tagging is constant ($s_i = s_{i+1}$). The estimate is based on two samples within a sam-

Table 82. Release (m_i) and recapture (r_{ij}) array for North Sea mackerel by area and year for the 1969 year class. NS denotes the North Sea south of 60°N, Sh the Shetland area. P_j = corrected production (millions of individuals), $(P_N)_j$ = corrected production of North Sea mackerel, S_i = yearly survival, R_j = yearly recruitment, $\tilde{z}_i = -\ln S_i$, $I_i = \ln R_j - \tilde{z}_i$, i = time of marking, j = time of recapture. See text.

Year of release	<i>i</i>	<i>m_i</i>	Year of recapture								$\sum_{j=i}^4 r_{ij}$	$\sum_{j=i+1}^4 r_{ij}$	<i>S_i</i>	<i>z_i</i>	<i>I_i</i>
			1970/1971		1971/1972		1972/1973		1973/1974						
			$j=1$ NS	Sh	$j=2$ NS	Sh	$j=3$ NS	Sh	$j=4$ NS	Sh					
1970.....	1	1 085	32	4	9	3	11	9	19	4	91	55	0.53	0.65	0.33
1971.....	2	6 900			113	36	113	109	232	64	667	518	(0.82)	0.20	0.28
1972.....	3	9 447					131	108	401	93	733	494	0.72	0.32	− 0.21
1973.....	4	4 642							301	34	335				
$i=j$ $\sum_{i=1} r_{ij}$			32	4	122	39	255	226	953	195					
$i=j-1$ $\sum_{i=1} r_{ij}$					9	3	124	118	652	161					
<i>P_j</i>			39.6	7.5	24.3	17.8	52.3	51.9	120.3	75.2					
<i>p_j</i>								0.96		0.40					
<i>(P_N)_j</i>								49.8		30.1					
$\sum (P_N)_j$			47.1		42.1		102.1		150.4						
$i=j$ $\sum_{i=0} r_{ij}$			36		161		481		1148						
$i=j-1$ $\sum_{i=0} r_{ij}$					12		(242)		813						
<i>R_j</i>			2.68		1.61		(1.12)								
ln <i>R_j</i>			0.98		0.48		0.11								

pling period, one from the area of release (North Sea south of 60°N in autumn) and one from an outside area some 10 months later (North Sea north of 60°N). The samples from 1972/1973 do, however, provide an exception. In this year the purse seiners were not allowed to fish mackerel in the area south of 59°N. The bulk of the tagged fish of the 1969 year class were released farther south, and both samples in 1972/1973 were drawn outside the tagging area, resulting in a considerable under-representation of recoveries from the 1972 releases. The first year's recoveries of these samples are therefore excluded in the calculation. The figures involved are given in brackets in Table 82.

The quantity p_j represents the fraction of the Shetland catch originating from the North Sea stock as calculated according to Equation (8); $\sum (P_N)_j$ is the total production of North Sea mackerel in sampling period j , from which the tags $\sum r_{ij}$ are recovered. On the basis of these figures the recruitment coefficient R_j is calculated according to Equation (4), and converted to the corresponding figure in instantaneous terms ($\ln R$). The column I_i shows the net increase ($I > 0$) or decrease ($I < 0$) in the catchable stock ($I_i = \ln R_j - z_i$ for $i = j$).

The estimated low survival of tagged fish in 1970

($S = 0.53$) is certainly not valid for the population. Although the number of tagged and recovered fish is small, the estimate is significantly lower than the survival estimate in 1971; the difference cannot be explained by fishing. The most likely explanation may be found in the coefficient of mortality caused by tagging. These relatively small fish (20–30 cm) may die more frequently owing to the tagging operation than larger individuals normally do.

The estimated recruitment of the 1969 year class to the purse-seine fishery indicates that a year class may be fully recruited at an age of three years. The p -estimates indicate no significant mixing with other stocks in the northern area with respect to the younger age groups, whereas age groups from other stocks may dominate the Shetland catches at an age of four years.

Table 83 summarizes the data for the age groups older than the 1969 year class. In 1969 and 1970 the survival estimates are low, but the restrictions on the fishery in 1971/1972 led to an improvement in the survival rate of the stock. In 1972 the recruitment to these older age groups rose to an unexpectedly high level ($R = 3.38$), indicating immigration of fish from other spawning areas.

Table 83. Release (m_i) and recapture (r_{ij}) array for North Sea mackerel by area and year for year classes older than the 1969 year class. See Table 82.

Year of release	<i>i</i>	<i>m_i</i>	Year of recapture										$\sum_{j=i}^4 r_{ij}$	$\sum_{j=i+1}^4 r_{ij}$	<i>S_i</i>	\tilde{z}_i	<i>I_i</i>
			1969/1970		1970/1971		1971/1972		1972/1973		1973/1974						
			$\overset{j=0}{\text{NS}}$	Sh	NS	Sh	$\overset{j=2}{\text{NS}}$	Sh	NS	Sh	NS	Sh					
1969.....	0	4 187	547	15	195	47	6	4	5	22	2	8	851	289	0.30	1.20	−0.54
1970.....	1	2 420			431	30	10	6	19	23	27	13	559	98	0.48	0.73	−0.37
1971.....	2	2 450					41	21	36	35	52	23	208	146	0.72	0.33	0.89
1972.....	3	2 126							44	32	80	21	177	101	0.58	0.54	−0.43
1973.....	4	1 518									106	18	124				
$\sum_{i=j}^j r_{ij}$			547	15	626	77	57	31	104	112	267	83					
$\sum_{i=j-1}^j r_{ij}$					195	47	16	10	60	80	161	65					
<i>P_j</i>			307.2	41.5	212.7	170.5	8.6	60.2	32.3	204.6	62.9	114.7					
<i>p_j</i>				(0.20)		0.30		0.09		0.21		0.22					
(<i>P_N</i>) _{<i>j</i>}				(8.3)		51.2		5.4		43.0		25.2					
$\sum (P_N)_j$			315.5		263.9		14.0		75.3		88.1						
$\sum_{i=j}^j r_{ij}$			562		703		88		216		350						
$\sum_{i=j-1}^j r_{ij}$					242		26		140		226						
<i>R_j</i>				1.94		1.43		3.38		1.12							
ln <i>R_j</i>				0.66		0.36		1.22		0.11							

STOCK STRUCTURE, MORTALITY, AND MIGRATION

Tables 84 and 85 show the estimated survival of tagged mackerel for the respective age groups according to Equation (6), disregarding mortality caused by the marking and the calculated stock size N according to Equation (5). The rows marked C_j show the total catch of the North Sea stock; N and C are given in millions of individuals. The catch figures are obtained by adding together the Norwegian catch in the North Sea south of 60°N and the calculated part of the Shetland catch originating from the North Sea; see Equation (8). To this catch figure are added catches of other nations in the same proportion as the total catch derived from Table 75.

Calculated s -values as a function of M according to Equation (7) are illustrated graphically in Figure 173. The basic data used are taken from Tables 84 and 85 for the periods 1971/1972 and 1972/1973 for the year class 1969, and for the periods 1969/1970, 1970/1971, 1971/1972, and 1972/1973 for the age groups older than the 1969 year class. If s and M were constant parameters, one would expect a common crossing area of all the curves in Figure 173, framed by a reasonable range of random variation in the calculated parameters. This is not the case, and since the s -value

should be a random variate, according to the nature of this parameter, the explanation is to be sought in the nature of M .

In 1972 the age groups older than the 1969 year class received recruits which could hardly be explained by normal recruitment to a self-sustained stock. Mackerel tagged and released in the spawning area of the Celtic Sea have been recaptured in large numbers in the Shetland area and also in the eastern North Sea. These findings show that immigration of mackerel to the North Sea from other areas does occur. It is therefore reasonable to assume that migration of mackerel also takes place from the North Sea into areas not fished by the Norwegian seiners. In that case the M -parameter includes not only natural death, but also the fraction of emigrating fish, which may vary with time and with age of the fish. Thus:

$$Z_i = F_i + (M + X_i) \quad (9)$$

where F_i is the fishing mortality, M the natural mortality, which is assumed to be constant, and X_i the coefficient of emigration which may vary with respect to the time period i and age.

In order to derive an estimate of s and $(M + X)$

Table 84. Estimated survival (m_{ij}) of mackerel tagged in the North Sea. N denotes the population size in millions of individuals; C , the corresponding total catch; S , survival. The data refer to the 1969 year class. See Table 82 and text.

Year of release	m_i	Year of recapture			
		1970-1971 $S = 0.53$	1971-1972 $S = 0.82$	1972-1973 $S = 0.73$	1973-1974 m_{i3}
1970....	1 085	1 085	575	472	344
1971....	6 900		6 900	5 658	4 130
1972....	9 447			9 447	6 896
1973....	4 642				4 642
$i=j$					
$\sum m_{ij}$		1 085	7 475	6 130	16 012
$i=0$					
$i=j$					
$\sum r_{ij}$		36	161	(242)	1 148
$i=0$					
$\sum (P_N)_j$		47.1	42.1	102.1	150.4
$N_{i/s}$		1 420	1 955	(2 586)	2 098
C_j			164	198	280
N_i		1 207	1 662	2 198	1 783

according to Equation (7), which in fact is the same as separating F and $(M + X)$ in the estimated \hat{Z} , at least two sets of data are needed; the accuracy of the estimate will be proportional to the difference in fishing mortality. Tables 84 and 85 show that the highest ratio of catch C to stock size N is found in the period 1970/1971 for the age groups older than the 1969 year class, and the lowest value of C/N occurs in the data of the 1969 year class in 1971/1972. Based on these two data sets, the graphical solutions of s and $(M + X)$ (the crossing of the respective curves in Fig. 173) correspond to 0.85 and 0.14 respectively.

The estimated s is reasonable and coincides with the test experiment on the survival of tagged fish. Even in the case of no emigration of fish ($X = 0$), the estimate of M is low compared with the M -value used in previous work on mackerel. It may however be noted that the fishing mortality of the age groups older than the 1969 year class in 1970/1971 was very high, resulting in a correspondingly narrow possible variation range in s and also in M (Figure 173).

Moreover, the estimates of \hat{Z} in the two cases are expected to be accurate because they are based on having a reasonably high number of recaptured tagged fish at liberty for a relatively long period. In the following, M has been set at 0.15.

Selecting a value of s of 0.85 and M of 0.15, the value of X for the various stock components concerned can be determined from Figure 173. The results are shown in Table 85 for the age groups older than the 1969 year class.

Table 85. Estimated survival (m_{ij}) of mackerel tagged in the North Sea. The data refer to year classes older than the 1969 year class. X_j denotes the coefficient of emigration; N_{xi} and N_{xi} , the calculated numbers of emigrating and immigrating fish; S , survival. See text.

Year of release	m_i	Year of recapture				
		1969-1970 $S = 0.30$	1970-1971 $S = 0.48$	1971-1972 $S = 0.72$	1972-1973 $S = 0.58$	1973-1974
		m_{i0}	m_{i1}	m_{i2}	m_{i3}	m_{i4}
1969....	4 187	4 187	1 256	603	434	252
1970....	2 420		2 420	1 162	836	485
1971....	2 450			2 450	1 764	1 023
1972....	2 126				2 126	1 233
1973....	1 518					1 518
$i=j$						
$\sum m_{ij}$		4 187	3 676	4 215	5 160	4 511
$i=0$						
$i=j$						
$\sum r_{ij}$		562	702	88	216	350
$i=0$						
$\sum (P_N)_j$		315.5	263.9	14.0	75.3	88.1
$N_{i/s}$		2 351	1 382	671	1 799	1 135
C_j		735	512	64	141	165
N_i		1 998	1 175	570	1 529	965
X_j		0.60	0	0.15	0.30	
N_{xi}		699	0	73	360	
N_{ri}		1 016	353	1 109	139	

The number of emigrating fish N_{xi} by periods may be calculated according to:

$$N_{xi} = E_{xi} N_i [1 - \exp(-z_i)] \quad (10)$$

where

$$E_{xi} = \frac{X_i}{F_i + M + X_i}$$

The rate of emigration E_x is the fraction of the total loss of fish in each period which migrate out of the area concerned. The calculated N_x according to Equation (10) is shown in Table 85. The bottom of the table shows the corresponding number of recruits N_r estimated according to the formula:

$$N_{ri} = \frac{N_i R'_i}{R_i - z_i} [\exp(R'_i - z_i) - 1] \quad (11)$$

where

$$R'_i = \ln R_j \quad \text{for } i = j.$$

The large emigration of mackerel observed among the older year classes in 1969 explains the high ratio of recoveries from the releases in 1969 in the Shetland area compared with those in the North Sea. The release in 1969 yielded about the same number of tags per unit of catch in both areas in 1972-1974,

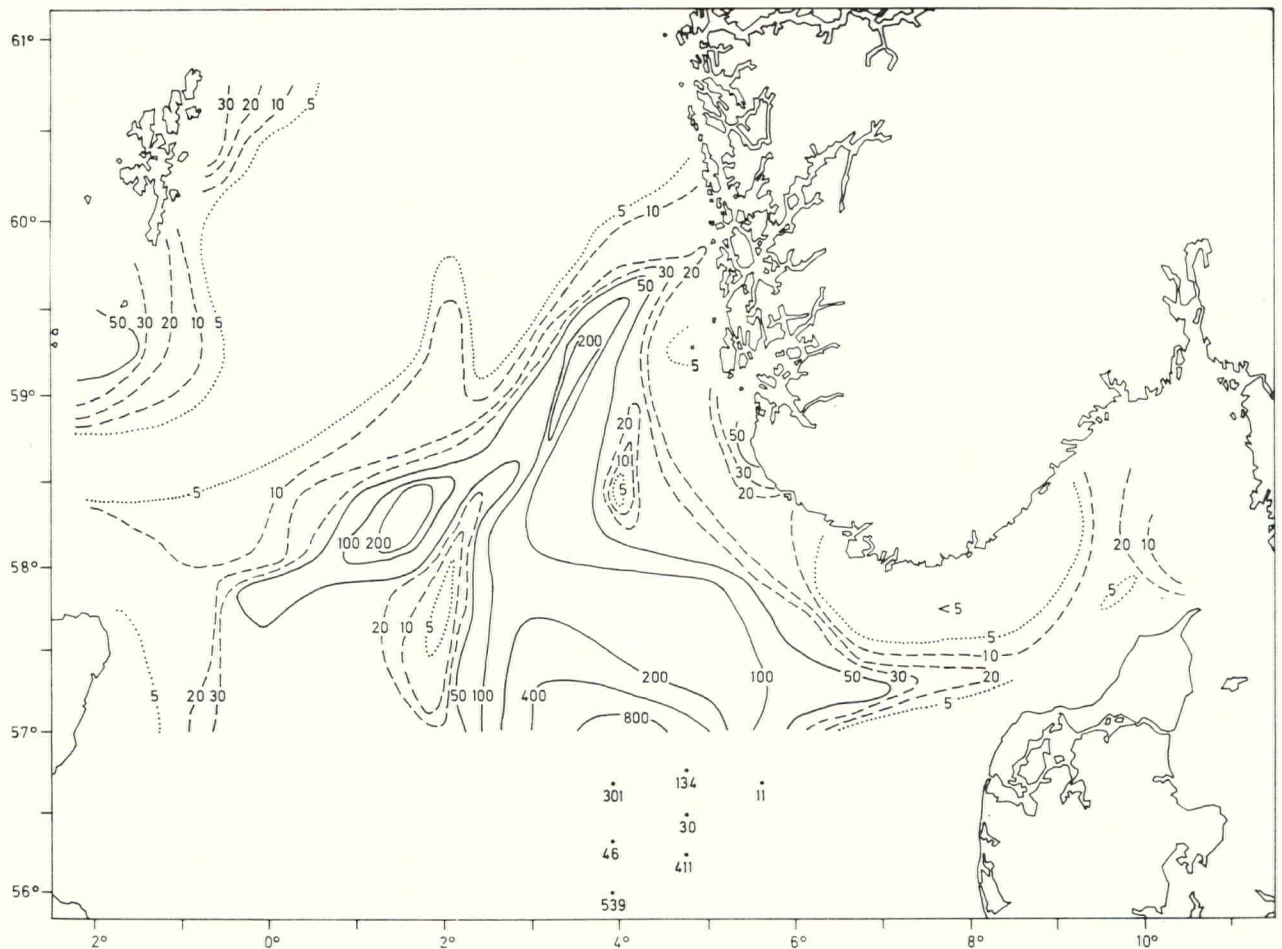


Figure 172. The distribution of mackerel eggs in the North Sea and the Skagerrak, 22 June to 3 July 1971. Isolines show the number of eggs per square metre of sea surface (Iversen, 1973).

which indicates that these old fish may now be mixed randomly throughout both spawning populations (Table 83).

Judging from the age composition of the North Sea stock in the autumn of 1970, fewer than half of the recruits in 1969/1970 may have come from recruiting age groups of the North Sea stock. This means that the exchange of individuals between stocks in this year was of the same order of magnitude (Table 86). On the other hand more than half of the recruits in 1970/1971 may have come from the 1968 year class, and although a certain immigration to the North Sea stock may have taken place, the interchange of individuals during that period was low. The year 1971 was the first with intensive fishing around Shetland, the area where the mixing of the stocks probably takes place. A high exploitation rate in the area through which the migration takes place may reduce the surviving part of the mixed stock,

and this may explain the reduced interchange of fish in 1971.

In 1972 the Shetland fishery was poor, and only 9 % of the catch was found to originate from the older age groups of the North Sea stock. The amount of mixing was very high, especially with regard to immigration, which corresponds to a biomass of about 500 000 tonnes. The highest catch in the Shetland area was obtained in the summer of 1973, corresponding to a low value of R . The estimated X -value is somewhat higher, indicating an increased rate of emigration. The accuracy of this estimate is, however, low because the estimate of the total mortality is based on only one sample of within-season recaptures. However, tag returns from recent catches indicate that an increased migration of mackerel out of the North Sea continued throughout the 1973/1974 season, including the 1969 year class, and a new winter fishery west of Shetland has developed. The recoveries

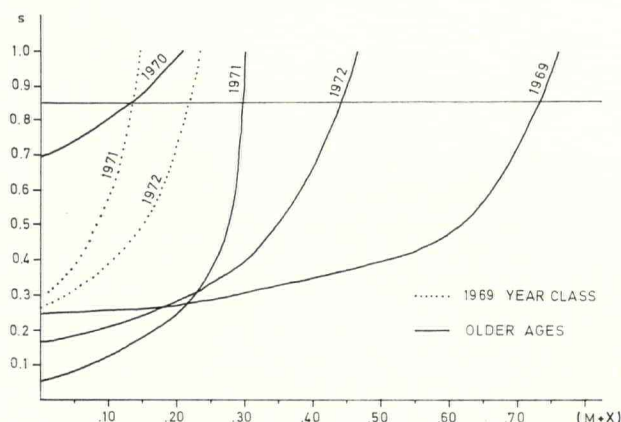


Figure 173. The mortality caused in tagging $(1-s)$ as a function of $M+X$ according to Equation (7). See text.

The present investigation covers too short a time period for any firm conclusions to be drawn about normal trends in the relationship between the North Sea mackerel and the mackerel spawning in the Celtic Sea. However, the present study indicates that the exchange of individuals between the stocks, especially in the older age groups, may be so extensive that they can hardly be treated as independent populations. It seems reasonable to assume that if one of the stocks is reduced by fishing, the net flow of individuals may run towards the exploited area until a new state of equilibrium is established, determined by the relative abundance of the two stocks. Under

STOCK SIZE AND EXPLOITATION

The year classes of 1966 and earlier are estimated in numbers according to Table 85 and the corresponding age composition in the purse-seine catch from the North Sea south of 60°N (Tables 76–80). Prior to 1969, these year classes were back-calculated in number by a cohort analysis using the Norwegian catches by age groups, raised by the ratio of the other nations' catch to the total. The 1967–1970 year classes are estimated in numbers from Tables 84 and 85, as three-year-old fish, i.e. when they are assumed to be fully recruited, and grouped according to the age composition (Tables 76–80) and back-calculated by a cohort analysis to age one. This procedure is adopted in order to reduce the error in the estimates due to mixing with other stocks.

As mentioned previously, the mixing of stocks may take place in the age groups older than three years. It is obvious that if the cohort analysis had been applied to back-calculate the year classes older than the 1969 year class from 1973 to 1969, these year classes would have been considerably overestimated as one-year-old fish. It may therefore be possible that a similar overestimate occurs in the year classes older

Table 86. Calculated stock size (N in millions of individuals) and fishing mortality (F) by year class for the North Sea mackerel stock in 1962–1973. P_3 denotes the stock size in 1 000 tonnes, including the age groups older than three years. See text.

Year class	1973-1972		1972-1971		1971-1970		1970-1969		1969-1968		1968-1967		1967-1966		1966-1965		1965	1964	1963
	<i>N</i>	<i>F</i>	<i>N</i>	<i>F</i>	<i>N</i>	<i>F</i>	<i>N</i>	<i>F</i>	<i>N</i>	<i>F</i>	<i>N</i>	<i>F</i>	<i>N</i>	<i>F</i>	<i>N</i>	<i>F</i>	<i>N</i>	<i>N</i>	<i>N</i>
1970	190	0.05	245	0.03	292														
1969	1 783	0.09	2 198	0.05	2 730	0.04	3 287												
1968	423	0.10	481	0.05	217	0.58	435	0.45	530										
1967	206	0.10	309	0.05	76	0.58	140	0.45	178	0.43	319								
1966	112	0.10	341	0.05	129	0.58	340	0.45	550	0.78	1 396	0.23	2 035						
1965	224	0.10	353	0.05	60	0.58	119	0.45	372	0.60	789	0.22	1 137	0.07	1 418				
1964	224	0.10	45	0.05	8	0.58	34	0.45	94	1.10	322	0.30	505	0.18	701	0.05	850		
1963	224	0.10	45	0.05	80	0.58	9	0.45	42	0.79	107	0.30	168	0.13	223	0.04	270	320	
1962	224	0.10	45	0.05	80	0.58	181	0.45	366	0.71	861	0.36	1 439	0.20	2 051	0.06	2 530	3 010	3 540
Older	224	0.10	45	0.05	80	0.58	181	0.45	372	0.96	1 130	0.56	2 307	0.38	3 909	0.14	5 280	6 440	7 760
ΣN	2 938	0.10	3 972	0.05	3 592	0.50	4 545	0.45	2 504	0.78	4 924	0.35	7 591	0.25	8 302	0.10	8 930	9 770	11 300
$\sum_{i=3}^{\infty} N_i$	2 938		3 727		570		823		1 796		3 209		4 419		6 183		7 810	6 440	0
P_3	1 258		1 482		247		445		938		1 468		1 913		2 692		2 866	2 190	0

than the 1966 year class, prior to the year 1969. Bearing in mind the calculated exchange of individuals in 1969/1970 when immigration was more or less compensated by emigration, it is, however, felt that before the accumulated North Sea stock was fished down in the late 1960's the immigration of mackerel from the western stock may have been balanced by emigration. In such a case the cohort analysis may also be valid for a mixed population.

The fishing mortality F in the period 1970/1971 to 1972/1973 was derived from the tagging experiments. For the period prior to 1970, F was derived from the cohort analysis. The last two lines of Table 86 show the stock size in number and weight excluding the age groups younger than three years of age. The stock size in weight is illustrated in Figure 174. Before the purse seine was introduced in the mid-1960's, the adult stock size may have fluctuated about a level of 2.5 million tonnes. The total catch in the North Sea prior to 1964 was below 100 000 tonnes, which corresponds to a fishing mortality below 0.04. The fishing mortality rose gradually from 1966 on and reached a peak of $F = 0.78$ in 1968/1969 (Table 86). In 1968 and 1969 even the one- and two-year-old fish were heavily exploited, which caused a very rapid decline in the stock.

Since 1970, the Norwegian industrial fishery has been regulated by a closed season from January to September in the North Sea area south of 60°N (59°N in 1970 and 1971), and by a catch-quota regulation of the autumn fishery in the eastern North Sea. This restriction, combined with good recruitment from the 1969 year class and immigration of older age groups in 1972, resulted in some recovery of the stock up to 1973. Subsequently, however, owing to poor recruitment from the 1970 and 1971 year classes, the stock size again declined.

In recent years the spawning stock has been somewhat larger than illustrated in Figure 174. Owing to an increased growth rate, the age of recruitment to the spawning stock has decreased, and in order to obtain a comparable estimate of the adult stock during the period concerned, a part of the two-year-old fish have to be included after 1970. This will raise the estimates of the adult stock in later years above the figures given in Table 86, especially in 1971 when the strong 1969 year class was recruited.

RECRUITMENT AND SUSTAINABLE YIELD

The recruitment of the 1962 to 1970 year classes as one-year-old fish is shown in bold print in Table 86. Two equally strong year classes were produced in 1962 and 1969. The weakest were the 1970 and 1971 year classes, amounting to about 300 million indi-

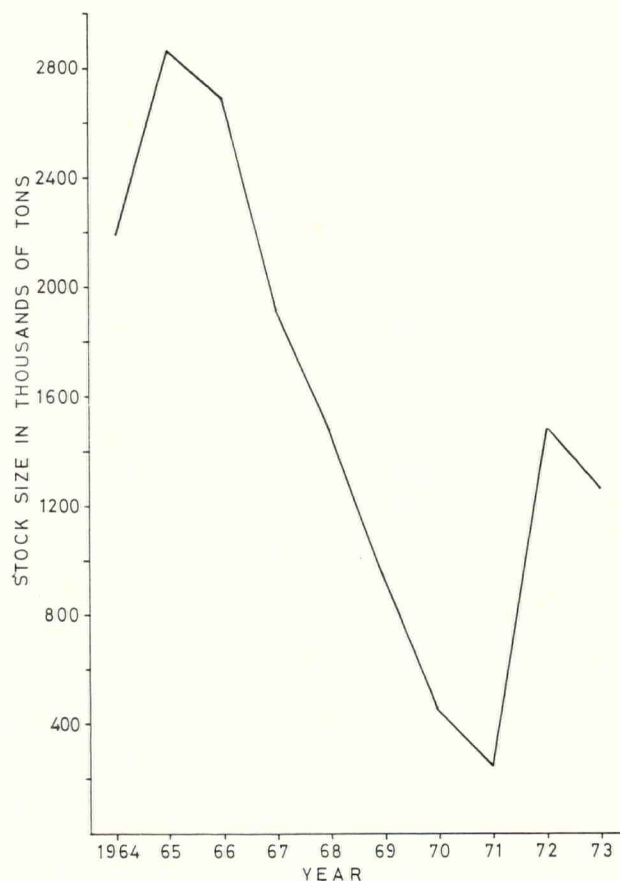


Figure 174. Estimated size of the North Sea mackerel stock from 1964 to 1973, including the age groups older than three years.

viduals as one-year-olds. The average recruitment from these ten year classes was 1290 million individuals. For a recruitment age of one year, $M = 0.15$ and a fishing strategy which regulates F to about 0.30, the maximum yield per recruit is about 200 g. This maximum yield per recruit is obtained when the bulk of the catch is taken during late summer and autumn (Hamre and Ulltang, 1972). The maximum sustainable yield (MSY) corresponding to this fishing strategy is about 250 000 tonnes per year. The corresponding equilibrium stock level is one million tonnes. This is about the same stock level from which the 1969 year class was recruited. Whether this estimate will be valid for the stock in the future depends mostly on the validity of the estimated average recruitment. In this respect it may be noted that the poor 1970 and 1971 year classes were recruited from a very small spawning stock, which may have affected the recruitment. An average recruitment from these two year classes would have increased the expected MSY to about 300 000 tonnes. The stock may

moreover be subjected to long-term changes in reproduction. According to an investigation of the abundance of mackerel available to the Dutch trawl fishery in the North Sea (Postuma, 1972), the recruitment in the mid-1950's may have been higher than in later periods. These observations indicate that an MSY of 250 000 tonnes for the North Sea mackerel stock may be a conservative estimate.

In the present study the two stocks occurring in the North Sea have been separated as far as the available data permit, and the estimated MSY refers to the North Sea stock only. It may, however, become a rather complicated task to assess the corresponding total allowable catch (TAC) of mackerel in the area concerned. The contribution to the catch from each of the stocks seems to be related to the relative abundance of the stocks and to the age composition of the populations. In order to approach a solution to these questions, a research programme monitoring the state of the western stock seems to be essential. A tagging programme for the Celtic Sea similar to that for the North Sea has therefore been initiated. Recoveries from these releases confirm a post-spawning migration of mackerel from the Celtic Sea into the area around Shetland and later in the season into the north-eastern North Sea. However, since there is no industrial fishery in the area of release, the recoveries so far obtained are probably insufficient for assessment purposes.

DENSITY-DEPENDENT CHANGES IN STOCK DISTRIBUTION AND GROWTH

DENSITY-DEPENDENT DISTRIBUTION

According to Postuma (1972), a decreasing catch per unit of effort in the Dutch trawl fishery for mackerel in the North Sea was correlated with a decreasing area of fish distribution. A similar development has been observed in the traditional Norwegian mackerel fisheries.

Before the introduction of the purse seine, mackerel were regularly fished in inshore and offshore waters, from the coast west of Bergen to the border of Sweden from early spring to late autumn. In the late 1960's the mackerel more or less disappeared from inshore waters, and the catch in offshore waters decreased considerably in the eastern Skagerrak and the Oslo-fjord. The inshore fishery based on beach seining terminated. The gillnet and hook-and-line fishery were concentrated in waters off the south and west coasts. The disappearance of spawning mackerel in inshore waters resulted in a similar absence of juvenile mackerel, which in previous years occurred regularly in the fjords in autumn. As a whole, the area of distribution of the spawning stock seemed

to shrink in the direction of the main spawning area located in the central and eastern North Sea (Figure 172).

The declining stock size had, on the other hand, no visible effect on the availability of mackerel to the purse seiners operating on the Reef south and west of Egersund. In October 1969, for instance, the seiners landed about 200 000 tonnes of mackerel from this area. This catch record was obtained from a rather depleted stock. These observations indicate that although the area of distribution was greatly reduced, the abundance of mackerel on the main fishing grounds in the North Sea may not have been reduced in proportion to the stock size. Therefore purse seiners may also profitably fish mackerel on a heavily over-exploited stock—which enlarges the danger of serious overfishing.

DENSITY-DEPENDENT GROWTH

Table 87 shows observed length by age for the strong 1962 and 1969 year classes at ages 3, 4, and 5. The 1962 year class was recruited before the accumulated stock was fished down, the 1969 year class when the stock was at a minimum. The observed differences in mean length are significant within a 95 % confidence limit.

The condition factor c is determined according to the formula:

$$c = w \times 10^3 / \bar{l}^3 \quad (12)$$

where w is the weight of the fish in g and \bar{l} the mean length in cm. The estimated c -values by year class and age are shown in Table 87. The table shows that in all three age groups, the condition factor is higher for the 1969 year class than for the 1962 year class. The growth difference in weight is thus even larger than the observed growth difference based on length.

The increased growth rate observed in the 1969 year class compared with the 1962 year class may be explained by the reduced stock.

Table 87. Length by age and condition factor (c) of the 1962 and 1969 year classes. Samples drawn in autumn; n denotes the number in the sample; \bar{l} , the mean length; and $S(l)$, the standard deviation

Age	1962 Year class				1969 Year class			
	n	\bar{l}	$S(l)$	c	n	\bar{l}	$S(l)$	c
3	51	34.5	1.20	8.23	132	34.8	0.97	8.80
4	63	35.6	1.67	9.06	135	36.1	1.26	9.31
5	188	36.6	1.34	8.75	270	37.2	1.21	9.05

SUMMARY

The paper deals with biological aspects and exploitation of the mackerel stocks occurring in the North Sea.

The state of stocks and exploitation in the North Sea area are investigated on the basis of annual releases of tagged fish and samples of commercial catches. Two populations occur, one spawning in the North Sea, the other in the Celtic Sea. The stocks are quite mixed, especially in the older age groups.

Following the introduction of the purse-seine fishery, the North Sea stock (age three years and older) was fished down from a level of 2.5 million tonnes in the early 1960's to about 250 000 tonnes in 1971. Since 1970 the fishery has been regulated, resulting in some recovery of the stock (Figure 174).

The recruitment of the 1962 to 1971 year classes has fluctuated within the range 12:1. Assuming a recruitment level equal to the average recruitment of these year classes, the maximum sustainable yield (MSY) of the North Sea stock is estimated at 250 000 tonnes per year.

The distribution area of mackerel is found to be related to stock size. The decline in stock size resulted in the disappearance of mackerel from fishing grounds previously exploited by conventional gears, whereas the availability of mackerel to the purse seine in off-shore waters is only slightly affected.

Density-dependent growth is indicated by an increased growth rate of the 1969 year class compared with that of the 1962 year class.

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