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BIOLOGY, EXPLOITATION, AND MANAGEMENT OF THE NORTHEAST ATLANTIC MACKEREL

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IDENTITY

The main distribution area of mackerel *Scomber scombrus* L. extends from the Bay of Biscay, along the continental shelf west of the British Isles, and the English Channel, to the North Sea and the Skagerrak. The widest distribution occurs during the feeding migration in summer when mackerel may be found around the Faroe Islands and at the southern coast of Iceland, along the Norwegian west coast north to the Lofoten area, and in the Kattegat and the southern part of the Baltic. 0-group mackerel have also been found during the international 0-group survey of the western Barents Sea.

In this area there are two separate spawning stocks: the Western stock, with its centre of spawning in the Celtic Sea, and the North Sea stock, which spawns in the North Sea and the Skagerrak (Anon., 1977).

Although groups of mackerel with different growth patterns have been described for the North Sea area (Nedelec, 1958), the results of tagging provide conclusive evidence for treating the mackerel in the North Sea and the Skagerrak as one stock unit. During the summer feeding migration the North Sea area is invaded by mackerel belonging to the Western stock. Whether mackerel born in the Celtic Sea also spawn in the North Sea still remains to be proven.

In the western area several stock components have been suggested. Bolster and Burd (1972) have identified two separate stock components in the Channel area, one overwintering and spawning in the Celtic Sea and one overwintering off the Cornish peninsula and spawning in the southwestern North Sea. Lockwood and Johnson (1976) have suggested that the fish on the Cornish coast might be an offshoot of the stock overwintering in the Celtic Sea. This view is supported by tagging results which also show that the mackerel spawning in the Bay of Biscay belong to the same stock (Bolster, 1974). The interchange of spawners among the various groups found in the western area and in the English Channel is thus so large that the mackerel in the entire area are assessed as one single stock unit (Anon., 1975).

AREA AND TIME OF SPAWNING

Johnson (1977) has summarized the available information on mackerel spawning in the North Atlantic. On the eastern side, three main areas were identified: the Bay of Biscay, the Celtic Sea, and the North Sea including the Skagerrak (Fig. 1). There is further evidence of spawning to the west and northwest of the British Isles, in the Channel area, and in the southwestern part of the North Sea. These latter spawning areas are most probably utilized by spawners belonging to the Western stock.

In the North Sea the main spawning takes place in the central and eastern parts and in the Skagerrak, with a clear-cut boundary of the egg distribution towards the north and northwest (Iversen, 1977). The boundary of the egg distribution towards the south and the southwest is less distinct and overlaps the spawning area in the English Channel (Fig. 2).

Spawning commences first in the Bay of Biscay and in the Celtic Sea, lasting from March to July with a peak in May/June (Fig. 11). In the Channel area and the southwestern North Sea the spawning is somewhat later and is closer in time to the spawning in the central North Sea. The intensity of spawning with time, in the North Sea, is illustrated in Figure 3. According to Cooper (1949), the timing of spawning is determined by the temperature in the wintering area, high temperatures being correlated with an early spawning season.

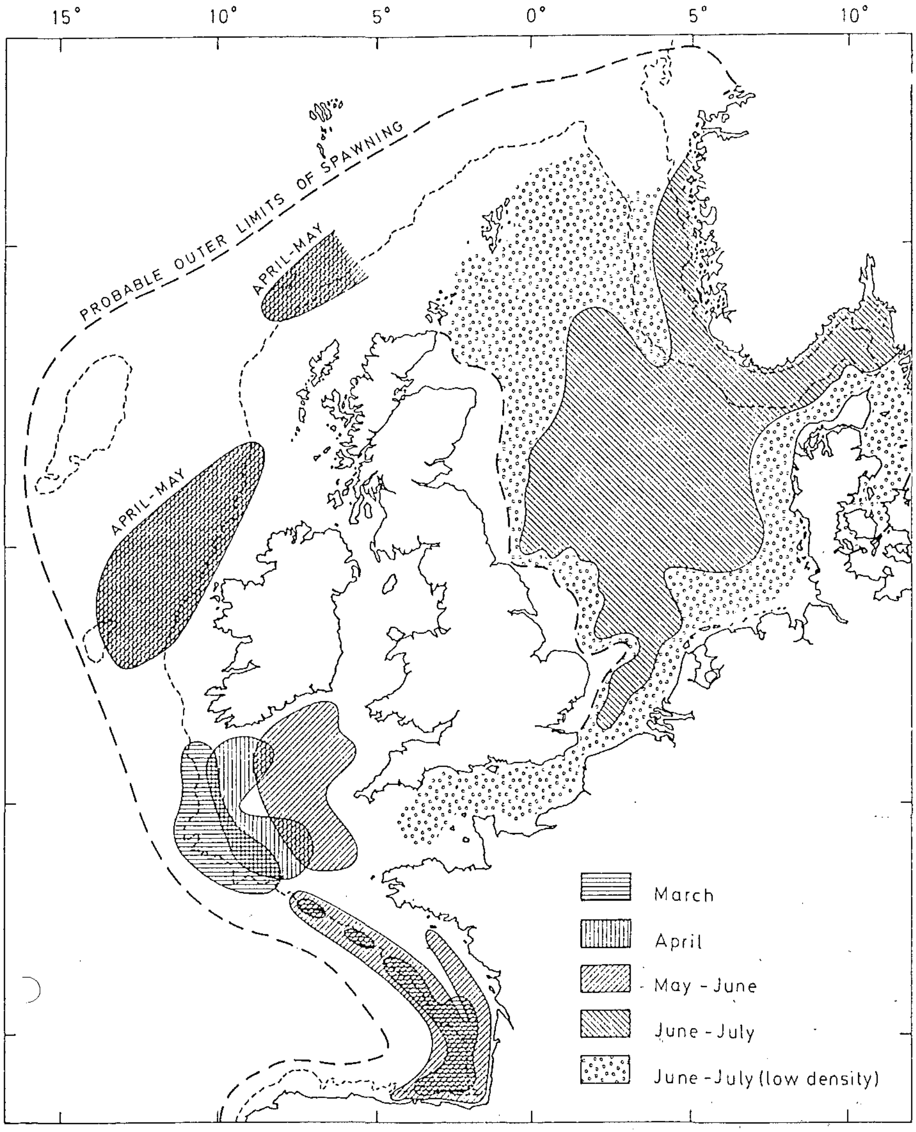

Figure 1. Principal mackerel spawning areas (Johnson, 1977).

FEEDING AREAS AND SEASONAL MIGRATION

JUVENILES

Little is known about the distribution of 0-group mackerel. The early larval stages are found in the area of spawning, but little is known about larval drift and the migration of 0- and 1-group mackerel. 0-group mackerel occur occasionally in late autumn along the coast of the Skagerrak and the eastern North Sea. 1- and 2-group mackerel have been caught close to the surface by purse seiners on the Danish Reef in summer. In winter 1- and 2-group mackerel are found in bottom-trawl catches over a wide area in the central North Sea and along the western edge of the Norwegian Trench (Walsh, 1977). Bolster (1974) states that the young mackerel of the Western stock are scarce in catches by English trawlers and drift netters but are occasionally seen in inshore waters in summer.

ADULTS

Before the large-scale fishery for mackerel developed in offshore waters, it was generally thought that mackerel migrated into coastal waters for spawning and feeding in spring and summer, and returned to offshore waters in autumn for wintering. The ob-

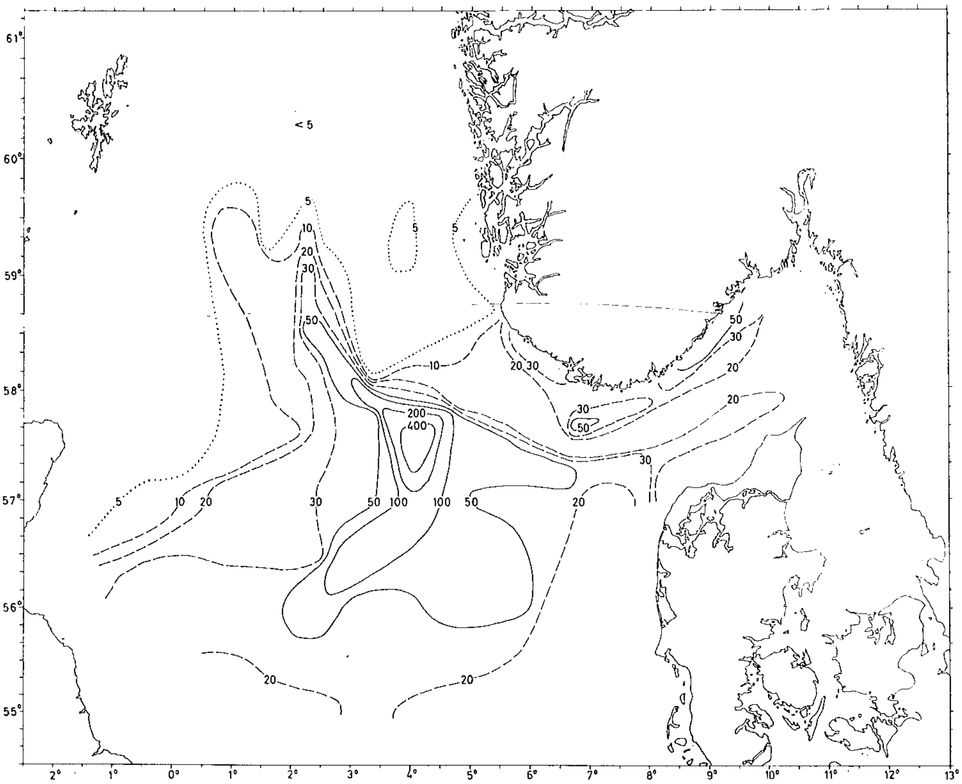

Figure 2. Horizontal distribution of mackerel eggs without visible larval embryo in 1974 (Iversen, 1977).

served density distribution of mackerel eggs and the development of the mackerel fishery in recent years show that the mackerel are mainly distributed in offshore waters throughout the year. In the North Sea the spawning period coincides with maximum intensity of feeding (Fig. 4), and the main spawning areas are therefore the main feeding areas. From the available information on seasonal changes in areas of fishing and on the basis of results from tagging (Agger, 1974; Bolster, 1974; Hamre, 1978; Lindquist and Hannerz, 1974) a pattern of seasonal migration emerges.

The North Sea stock that overwinters in the north-western part of the Norwegian Trench and on the shelf west of Shetland moves southward and eastward during April/May towards the spawning grounds in the central North Sea and the Skagerrak. During this migration the mackerel frequently occur in dense schools, thus becoming available to purse seining. The schools disperse when the fish approach maturity in early June.

After spawning, the North Sea stock disperses over a wide area in the North Sea, and in July/August the fish may occur in the Kattegat, in the southern Baltic, and on the Norwegian west coast as far north as Lofoten. A major component of the stock seems to migrate to the bank area of the northern North Sea, particularly to the area north and east of Shetland where North Sea mackerel are caught together with mackerel coming from spawning grounds in the Celtic Sea. In September the North Sea mackerel return to the bank area in the eastern North Sea from the Baltic, Kattegat and Skagerrak, and from the northern North Sea. Here they congregate in late autumn before descending to deeper waters for wintering. It was on the basis of these large autumn concentrations that the extremely rich purse-seine fishery developed in the late 1960s.

The Western mackerel stock, overwintering in the Celtic Sea and off the Cornish coast, starts its spawning and feeding migration in March. The mackerel move south to spawn in the Bay of Biscay and north to the area off the Hebrides; but the bulk of the stock spawns in the Celtic Sea. A major component of the stock which overwinters off the Cornish coast moves eastward through the English Channel and is found spawning and feeding in the southern parts of the North Sea in summer and autumn (Bolster and Burd,

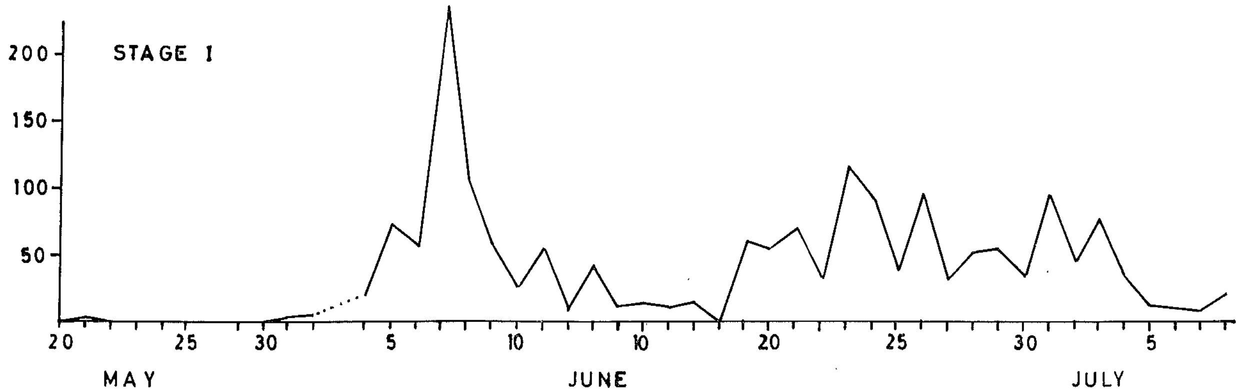

Figure 3. Number of mackerel eggs spawned each day at Ekofisk (central North Sea) in 1977 (Bakken et al., 1977).

1972; Bainbridge et al., 1974). Recent recoveries of mackerel tagged off the Cornish coast in 1975 (British releases) and retained in Norwegian meal plants in 1976 and 1977, demonstrate that Cornish mackerel also migrate into the central and northern North Sea.

After spawning in the Celtic Sea, a major component of the Western stock migrates north and appears in the area around Shetland in late July. By August/

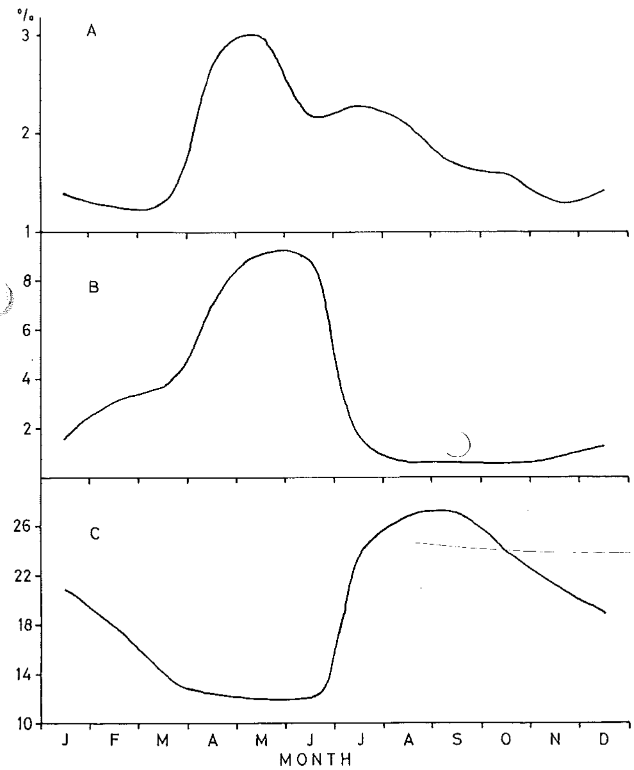

Figure 4. Monthly indices of feeding (A), gonad weight (B), and fat content (C) for North Sea mackerel (Hamre, 1978).

September, the Western stock has formed the main basis for the rich summer fishery which has taken place in this area since 1969. The older age groups dominate the summer catch in the Shetland area, both from the Western stock and the North Sea stock (Table 1).

It can be concluded that the adult mackerel is a highly migratory fish whose range of migration covers the main distribution area in the Northeast Atlantic. The degree of mixing of the two separate stocks assumed to exist may be considerable. The mixing seems to take place during the feeding period, but to what extent the mackerel separate in autumn and return to their original overwintering and spawning areas is not yet known.

AGE AND GROWTH

Mackerel have been aged by counting zones in scales and otoliths. The scales are relatively small, and otoliths have therefore been preferred in age reading (Nilsson, 1914; Steven, 1952; Kändler, 1957; Aker, 1961; Castello and Hamre, 1969; Postuma, 1972; and Bolster, 1974). There is no disagreement in the interpretation of the zones, but the difficulties in ageing old fish vary. Postuma (1972) found that reliable readings could be obtained up to an age of 5 years, whereas Bolster (1974) made readings up to 10 years. In the Norwegian sampling programme of the age composition of the catches the age groups above 7 years are grouped, owing to the difficulties encountered in the age reading of older specimens.

Length at age data published by various authors for the two stocks respectively (tip of nose to tip of tail measurements) are given in Table 2. Mackerel are fast growing, especially in the younger age groups; and the growth of North Sea mackerel takes place during a relatively short period in summer and early autumn. In comparing growth data, accurate timing

Table 1. Age distribution (%) in Norwegian purse-seine catches, 1969–1977. Shetland area (Sh), northeastern North Sea (NS). Figures in parentheses indicate fish older than 7 years (6 years in 1969)

Year	1969	1970		1971		1972		1973		1974			1975		1976	1977
class	NS	Sh	NS	Sh	NS	Sh	NS	Sh	NS	SH	NS	Rona	Sh	NS		
1975	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6·1
1974	–	–	–	–	–	–	–	–	–	–	–	–	–	2·2	5·8	14·1
1973	–	–	–	–	–	–	–	–	–	0·1	0·6	0·9	0·9	1·6	5·4	20·2
1972	–	–	–	–	–	–	–	–	0·5	0·3	5·4	5·0	4·9	3·8	1·6	3·5
1971	–	–	–	–	–	–	0·1	0·1	2·4	4·2	7·9	3·9	3·8	9·8	20·3	16·2
1970	–	–	–	–	0·9	0·9	1·4	3·9	5·5	7·6	11·6	9·4	9·4	6·7	3·2	6·4
1969	–	–	15·7	4·2	74·1	21·9	64·8	19·4	60·6	34·8	57·6	65·0	65·0	55·5	35·9	(33·5)
1968	3·8	5·7	25·2	9·0	9·5	14·0	10·6	19·4	13·6	13·0	7·9	7·1	7·1	5·6	(27·8)	–
1967	6·5	5·4	10·0	11·2	3·4	12·1	6·8	7·7	6·6	7·1	1·3	2·7	(8·7)	(14·0)	–	–
1966	27·9	18·1	24·4	24·8	5·6	13·2	7·5	13·0	3·6	(32·9()	(7·7)	(6·0)	–	–	–	–
1965	18·2	20·1	8·5	24·5	2·6	14·7	7·8	(36·5)	(7·2)	–	–	–	–	–	–	–
1964	4·7	9·7	2·5	5·0	0·4	(23·2)	(1·0)	–	–	–	–	–	–	–	–	–
1963	2·1	7·4	0·7	(21·3)	(3·5)	–	–	–	–	–	–	–	–	–	–	–
	(36·8)	(33·6)	(13·0)	–	–	–	–	–	–	–	–	–	–	–	–	–

of the samples is therefore essential. The data on observed length at age in Table 2 do not correspond exactly with respect to time of sampling, and taking this into account, the table indicates that the stock of the Western area has more or less the same yearly growth as the stock in the North Sea, reaching some 35 cm at an age of 4 years. There is a difference in the growth pattern with respect to the seasonal variation. Steven (1952) states that about half the yearly increment in length of mackerel in the Western area is put on during the months September–April, whereas Castello and Hamre (1969) found practically no growth in length of the North Sea mackerel from August to May. The large seasonal variation in growth of the North Sea stock has been an important factor in the management of the mackerel fishery in the North Sea.

Weight at age for the North Sea stock and the Western stock are given in Table 3 (Anon., 1978). These data refer to samples collected in recent years and are those used for the present assessment. Table 4 gives observed weight at age data for North Sea mackerel in the 1960s (Castello and Hamre, 1969). It is apparent that the weight at age of the North Sea stock has increased in recent years, compared with that in the 1960s. It is also apparent that the present weight at age of the Western stock broadly corresponds to that observed in the North Sea stock in the 1960s. Taking into account that the abundance of the Western stock has remained at a high level, this observation supports the suggestion of density-dependent growth in the North Sea stock demonstrated by Hamre (1978) in comparing the growth of the 1962 year class with that of the 1969 year class (Table 5). The weight at age data demonstrate the difference in seasonal growth of the two stocks observed in Table 2.

The age compositions of the purse-seine catches taken in the North Sea and Shetland areas are given in Table 1 for the period 1969–1977. In the North Sea the 1969 year class has dominated since 1971. Prior to 1971, the 1965 and 1966 year classes domi-

Table 2. Length (cm) at age data for Western and North Sea mackerel stocks, derived from various authors. Summer (S), autumn (A)

Age in years														
1		2		3		4		5		6		7		Source
S	A	S	A	S	A	S	A	S	A	S	A	S	A	
Western stock														
23·8	28·7	30·6	32·1	33·0	33·3	34·1	34·6	35·5	35·9	36·2	–	–	–	Steven, 1952
23·4		31·0		32·0		33·0		34·0		34·9		35·7		Bolster, 1974
North Sea stock														
–	26·7	28·6	32·0	31·9	34·4	34·0	35·1	35·3	34·6	35·6	36·6	36·1	38·4	Castello and Hamre, 1969
20·1	–	28·1	–	32·2	–	34·5	–	34·9	–	35·6	–	37·8	–	Postuma, 1972
26·3		30·6		33·8		35·0		35·7		36·21		38·2		Kändler, 1957

Table 3. Mean weight (g) at age of mackerel by quarter. Overall mean ($\overline{w}$) weighted by catches in recent years. (Anon., 1978)

		North Sea – Age in years 1	2	3	4	5	6	7	⩾ 8
Division IVa	Jan–Mar	123[a]	234	325	338	350	346	468	472
	Apr–Jun	–	206	309	362	423	437	481	553
	Jul–Sep	250[a]	334	367	393	441	455	523	588
	Oct–Dec	245[b]	334	342	393	424	463	503	521
	$\overline{w}$	245[b]	329	363	392	438	455	520	580

[a] Single fish only. [b] Based on Oct–Nov only.

		Western area – Age in years 0	1	2	3	4	5	6	7	⩾ 8
Sub-area VI	Jan–Mar					No data available				
	Apr–Jun	–	–	232	281	309	345	357	422	462
	Jul–Sep	–	203	275	284	343	432	431	483	617
	Oct–Dec	–	180	286	314	327	463	415	475	625
Sub-area VII	Jan–Mar	–	58	125	177	233	246	309	356	378
	Apr–Jun	–	107	147	186	257	277	285	336	356
	Jul–Sep	61	112	183	223	256	277	317	321	392
	Oct–Dec	65	125	181	209	275	327	373	411	509
	$\overline{w}$	64	112	169	207	269	318	362	398	505

Table 4. Mean weight (g) at age of mackerel by quarter in the North Sea and the Skagerrak. (Castello and Hamre, 1969)

		Age in years: 1		2		3		4		5		6		7		8		⩾ 8	
		n	g	n	g	n	g	n	g	n	g	n	g	n	g	n	g	n	g
Jan–Mar	1967	–	–	22	159	11	288	2	295	18	350	5	402	2	345	1	380	10	450
	1968	–	–	96	116	3	216	–	–	–	–	–	–	–	–	–	–	–	–
	1969	–	–	34	153	330	203	90	279	28	320	7	392	55	362	9	406	24	436
Total n and av. wt.		–	–	152	130	344	206	92	287	46	336	12	396	57	362	10	404	34	440
Apr–Jun	1967	–	–	10	158	18	302	4	352	43	359	12	356	12	381	14	372	74	421
	1968	–	–	8	211	87	340	48	399	15	468	100	451	33	517	17	532	98	566
	1969	–	–	7	192	124	275	101	345	36	401	10	435	91	417	34	495	79	515
Total n and av. wt.		–	–	25	184	229	302	153	362	94	390	122	440	136	55	475	475	251	507
Jul–Sep	1967	–	–	8	318	22	395	8	508	137	456	17	562	4	550	7	601	24	605
	1968	–	–	7	300	39	407	21	417	13	461	55	467	14	575	11	548	27	620
	1969	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total n and av. wt.		–	–	15	310	61	403	29	442	150	457	72	490	18	569	18	568	51	613
Oct–Dec	1967	97	132	91	281	46	364	15	454	188	429	39	471	39	527	33	513	72	530
	1968	22	171	93	242	23	334	6	370	3	360	18	447	–	–	1	440	11	493
	1969	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total n and av. wt.		119	139	184	262	69	354	21	430	191	428	57	464	33	527	34	510	83	525

Table 5. Length (cm) at age and condition factor (c) of the 1962 and 1969 year classes. Samples drawn in autumn. Mean length (l) and standard deviation $S(l)$. (Hamre, 1978)

Age	Year class 1962				Year class 1969			
	n	l	$S(l)$	c	n	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

nated together with the age groups older than the 1963 year class. The latter year classes dominated the Shetland catches up to 1974.

EXPLOITATION

ANNUAL CATCH

The annual catch of mackerel in the Northeast Atlantic is normally grouped into two areas. One is the North Sea area, including the Skagerrak, referring to the mackerel catch of the ICES statistical sub-areas II, IIIa, and IV. The other is the Western area including sub-areas VI, VII, and VIII. The catch statistics are thus not separated according to the assumed stock separation, since reported catches from the northern North Sea (division IVa) during summer and early autumn are mixed catches with a major contribution from the Western stock. The catches reported in division IVc may also originate from the Western stock. For assessment purposes the catches in IVa have been separated according to stocks using tagging data. It should be noted that the large-scale summer fishery for mackerel in the northern North Sea is of recent origin and that the catch statistics in areas excluding IVc prior to 1970 may correspond to catch of the two separate stocks. Table 6 gives the annual mackerel landings in the North Sea by country since 1965, and Table 7 the landings from the Western area. Figure 5 shows the development in the international Northeast Atlantic catch since 1946.

The North Sea catch increased slightly during the 1950s and exceeded 100000 tonnes in the early 1960s. From 1964 onwards the landings increased rapidly and reached a peak of 932000 t in 1967. This rise was due to the increased Norwegian catch. In the following two years the catch decreased slightly. A major drop in the Norwegian catch took place in 1969–1970, falling from 683000 t to 279000 t, owing to national regulation of the fishery. Since 1970 the Norwegian catch has been regulated by yearly catch quotas, and the total catch has fluctuated between 189000 and 348000 t. In recent years the Faroes have increased their mackerel catches to 63000 t in 1976 from nothing prior to 1968. With the exception of Denmark, other countries have had decreasing mackerel catches in recent years compared with the early 1960s.

The international mackerel catch in the Western area (Table 7) exceeded 100000 t in 1970. The catch increased gradually in the 1970s and reached 507000 t in 1976. Prior to the 1970s France and Spain had the

Table 6. Nominal catch (t) of mackerel in the North Sea, Skagerrak, and Kattegat (divisions IV and IIIa) 1965–1977. (Anon., 1978)

	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977[a]
Belgium	138	67	201	77	139	19	85	129	78	145	134	292	47
Denmark	6 509	7 552	20 282	9 887	10 851	26 753	17 590	2 023	7 459	3 890	9 836	27 988	21 823
Faroe Islands	–	–	–	–	3 080	2 134	3 603	7 551	11 202	18 625	23 424	63 476	41 123[b]
France	7 635	5 390	7 486	4 684	11 353	4 677	9 061	6 882	636	2 254	2 749	2 607	2 669
German Dem. Rep.	–	–	915	349	399	51	166	346	214	234	141	259	41
Germany, Fed. Rep.	2 221	1 501	2 132	1 353	1 161	225	407	374	563	270	276	284	3 867
Iceland	–	–	105	352	612	1 492	649	687	3 079	4 689	198	302	–
Netherlands	16 977	12 247	11 964	5 986	4 928	2 956	4 945	4 436	2 339	3 259	2 390	2 163	9 362
Norway[c]	156 605	484 428	866 548	779 084	683 045	278 631	200 635	160 141	298 877	255 132	241 533	207 867	182 200
Poland	3 695	2 294	2 261	1 629	12	205	130	244	561	4 520	2 313	2 020	298
Sweden	13 364	13 754	15 246	11 783	10 820	4 407	3 163	4 748	2 960	3 579	4 789	4 581[a]	3 522[d]
U.K. (England and Wales)	76	99	46	55	35	35	23	32	31	61	33	89	10
U.K. (Scotland)	1 019	618	742	583	231	148	616	395	2 943	390	578	1 199	1 590
USSR	227	1 778	4 098	6 094	12 516	718	2 600	611	17 150	8 161	9 330	1 231	2 784
Total	208 466	529 728	932 026	821 916	739 182	322 451	243 673	188 599	348 092	305 209	297 724	314 358	269 336

[a] Preliminary figures.
[b] Includes VI.
[c] Includes catches from IIa (1973: 21573 t; 1974: 6818 t; 1975: 34662 t; 1976: 10516 t; 1977: 1400 t).
[d] From ICES Data Form 5 (Jan–Dec).

Table 7. Nominal catch (t) of mackerel in the Western area (divisions VI, VII, and VIII). (Data for 1967–1976 as officially reported to ICES). (Anon., 1978)

	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977[a]
Belgium	7	2	11	8	2	1	3	7	17	10	–
Denmark	–	–	–	–	–	–	–	–	–	3	–
Faroe Islands	–	–	–	–	–	–	635	8 659	1 760	5 539	–
France	34 494	34 896	31 356	42 899	33 141	35 354	41 664	37 824	25 818	33 556	34 387
German Dem. Rep.	949	95	9	130	93	214	1 733	2 885	9 693	4 509	431
Germany, Fed. Rep.	333	613	428	783	258	98	559	993	1 941	391	4 249
Iceland	–	–	–	90	86	74	52	–	21	10	–
Ireland	2 245	2 164	1 615	1 055	3 107	4 592	8 314	8 526	11 567	14 305	18 585
Netherlands	3 859	2 597	4 441	3 828	3 837	6 166	7 785	7 315	13 263	15 007	27 723
Norway	–	–	–	–	1 611	–	34 600	32 597	1 907	4 252	200
Poland	520	1 518	2 149	6 054	10 832	13 219	10 536	22 405	21 573	21 375	2 240
Spain	27 863	20 753	21 571	31 368	37 506	31 416	25 677	30 177	23 408	18 480	18 000[b]
Sweden	–	–	–	–	–	–	–	–	–	38	2[c]
U.K. (England and Wales)	2 634	2 585	2 692	3 374	4 791	6 923	13 081	21 132	31 546	57 311	134 597
U.K. (N. Ireland)	158	151	279	243	315	57	93	75	30	95	3
U.K. (Scotland)	490	537	402	807	805	1 412	5 170	8 466	16 174	28 399	52 490
USSR	–	–	6 147	13 555	36 390	71 249	65 202	103 435	309 666	262 384	22 248
Total ICES	73 552	65 911	71 100	104 194	132 774	170 775	215 104	284 496	468 384	465 754	315 155
Bulgaria	–	–	–	–	–	–	4 341	13 558	20 830	28 195	–
Rumania	–	–	–	–	–	–	–	–	2 166	13 222	–
Total	73 552	65 911	71 100	104 194	132 774	170 775	219 445	298 054	491 380	507 178	315 155

[a] Preliminary. [b] Working Group estimate. [c] From ICES Data Form 5 (Jan–Dec).

largest mackerel catch in the Western area. The marked rise in recent years was caused by an increase in the USSR catch from 14000 t in 1970 to 310000 t in 1975. In 1977 the catch declined to 315000 t, owing to a dramatic cut in the USSR catch. By contrast, the UK landings increased considerably and now represent more than 50% of the total catch.

THE FISHERY

Prior to 1960, the mackerel in the North Sea were caught by gill net, hook and line, and trawl. Some catches were also taken by beach seiners and small purse seiners in inshore waters. Summer and autumn were the main fishing season for gill net and hook and line. The trawl fishery in the bank area of the North Sea directed at herring caught mackerel as by-catch during winter and spring in the overwintering area. In the late 1950s, trawlers from the Netherlands developed a regular mackerel fishery in spring, in the wintering area on the edge of the Norwegian Trench (Fig. 6). This fishery terminated in the late 1960s owing to a decrease in the abundance of mackerel available to that gear (Postuma, 1972).

Following the introduction of the hydraulic power block, Norwegian purse seiners started to fish for mackerel in the bank area of the central and eastern North Sea in 1963. Initially the North Sea purse-seine fishery was directed at herring only, but when the fishermen realized the low target strength of mackerel, and learned that relatively weak and indistinct echo-sounder traces could indicate large mackerel schools, mackerel became the major aim of the North Sea purse-seine fleet in autumn, and in spring before the schools dispersed for spawning.

Figure 7 shows the main fishing grounds of the purse seiners by season. The peak season in the non-regulated purse-seine fishery was September to October when the mackerel congregated on the reef before descending to deeper waters for wintering. Large catches of prespawners were also landed from this area in May and early June. The fishery in the wintering area in the Norwegian Trench fluctuated considerably, owing to varying availability of the schools to the purse seiners. The mackerel were distributed in deeper water layers during winter, often below the range of the purse net, in order to avoid the winter-cooled surface layers. When a school was caught and forced to the surface by pursing and hauling in the net, the fish swam downward, which resulted in much damage to the gear and loss of catch. The winter fishery was therefore of minor importance to the purse-seine fleet. Since this fishery also constituted the least efficient form of exploitation, owing to the growth pattern of the fish, the industrial winter fishery has been prohibited for Norwegian seiners since the end of the winter of 1969.

In the summer of 1969, Norwegian purse seiners

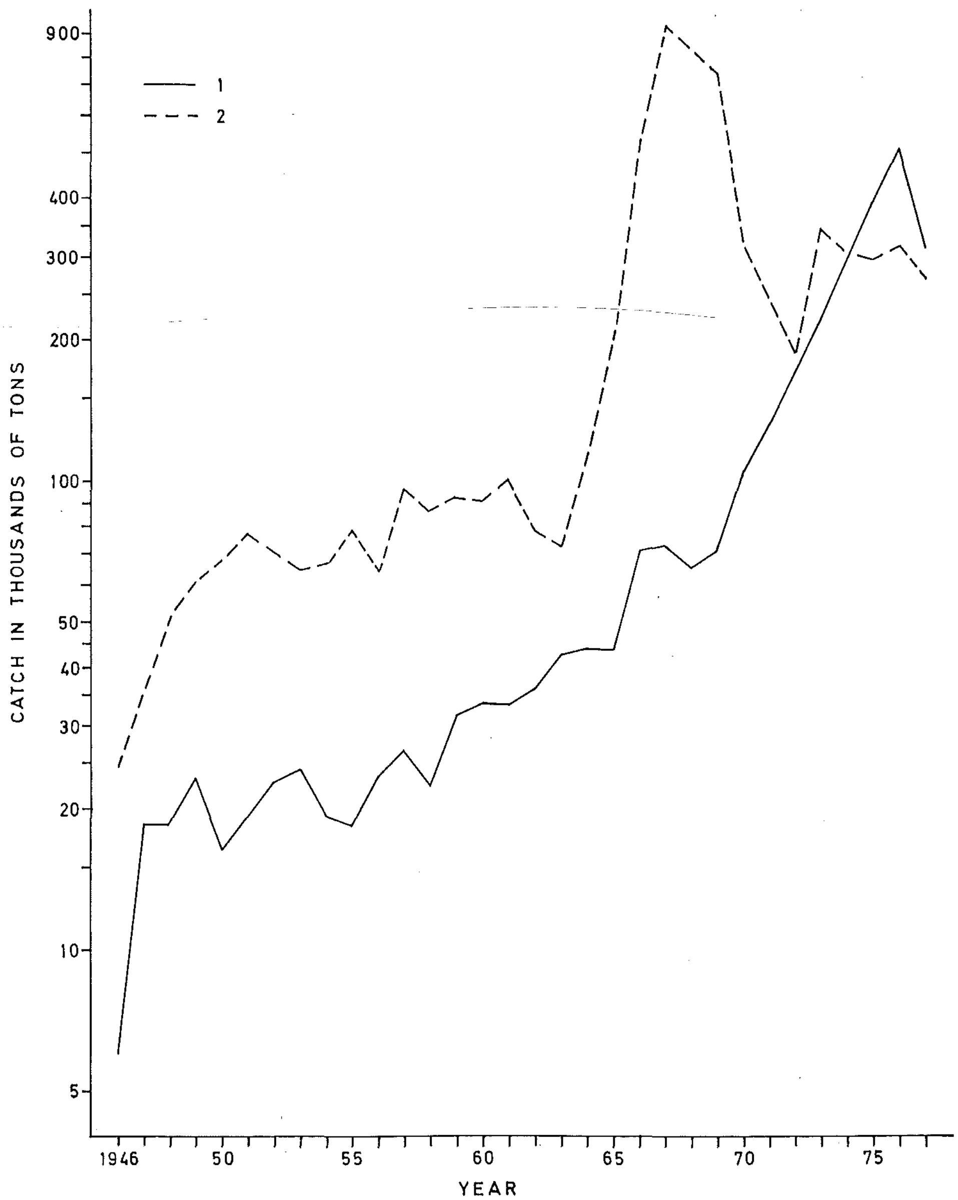

Figure 5. International catch of Northeast Atlantic mackerel, 1946–1977. 1) Western area, 2) North Sea area.

started to fish for mackerel in the northern North Sea, particularly in the area around Shetland. This later became a regular fishery, with the season lasting from mid-July until early September. As mentioned earlier, this fishery is based on mixed North Sea and Western mackerel.

Since the winter of 1974/1975 mackerel have been available to the purse seiners in the area between Shetland and Rona. The results from tagging and the age composition of the catch (Table 1) show that these are mostly overwintering mackerel of the North Sea stock. In order to apply the Norwegian protective measures in this area as well, the regulations for the Norwegian winter fishery were extended westward in 1975 to include division VIa.

Lockwood and Dann (1976) have reviewed the mackerel fishery in the Western area (sub-area VII) over the past fifty years. Until the 1960s most of the mackerel were caught by drifters, primarily English, French and Irish vessels. The fishery took place both

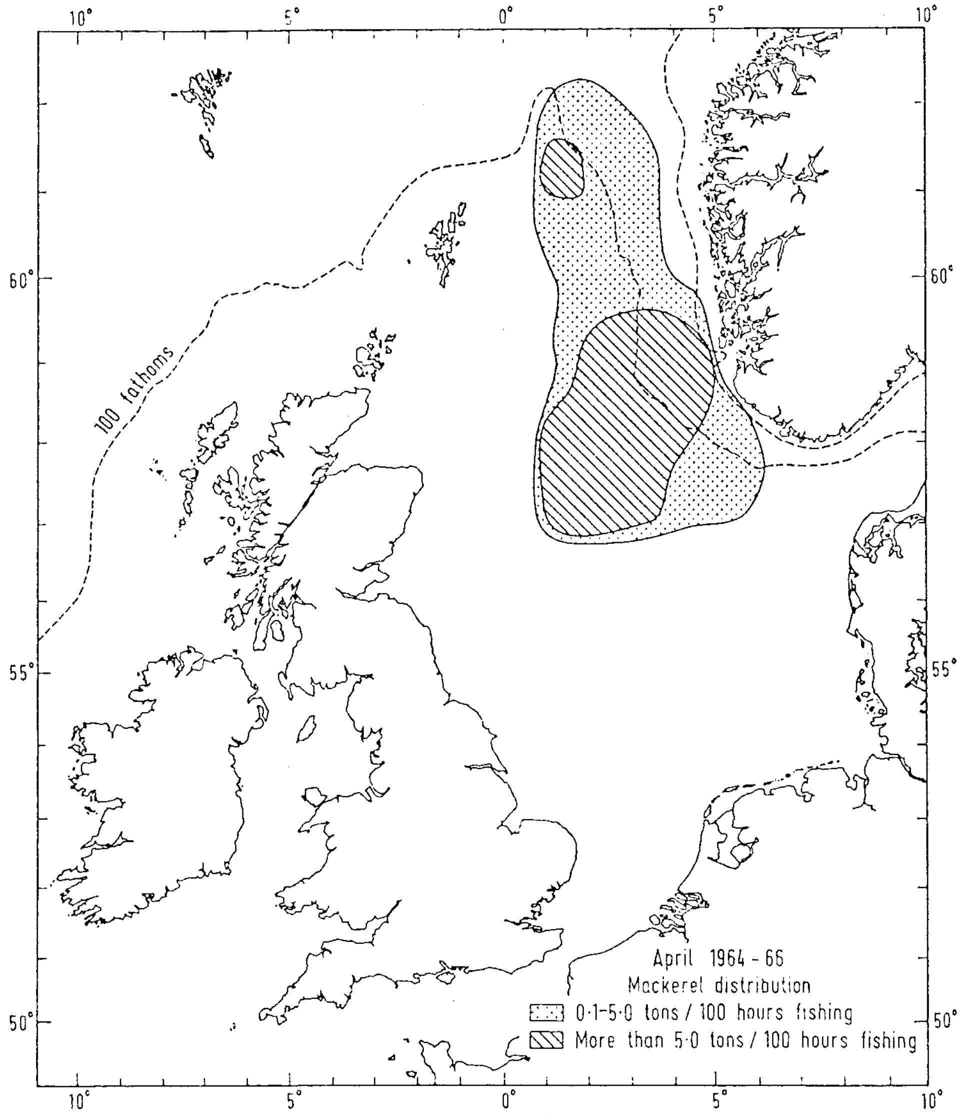

Figure 6. Mackerel distribution according to the catch per 100 h fishing by a Dutch standard trawler of 500 b.h.p. in April, 1964–1966. The dotted area represents a catch per unit of effort of 0·1–5·0 t; the striped area, a catch per unit of effort of over 5·0 t (Postuma, 1972).

in inshore and offshore waters. The inshore fishery took place along the Cornish coast in January–April, by local boats. The offshore fishery commenced in March off the south coast of Ireland. As the season progressed through April and May the main fishing area moved to the south, and the fishery was concluded in June in the eastern part of the English Channel. The limiting factor of this fishery was probably the market for fresh fish.

In the 1960s there was a gradual decline in the drift-net fishery but a steady increase in the pelagic-trawl and hand-line fisheries. Since 1966 the U.K. hand-line fishery has expanded dramatically owing to the occurrence of large concentrations of overwintering mackerel close to the Cornish coast. These schools begin to form in autumn and reach their maximum size and density in November/December. The overwintering mackerel disperse gradually in February/March. The regularity with which these schools appeared and their catch rate has led to a great expansion of the U.K. hand-line fishery, and in 1976 about 400 vessels under 12 m participated in it. The distribution area of these mackerel is shown in Figure 8.

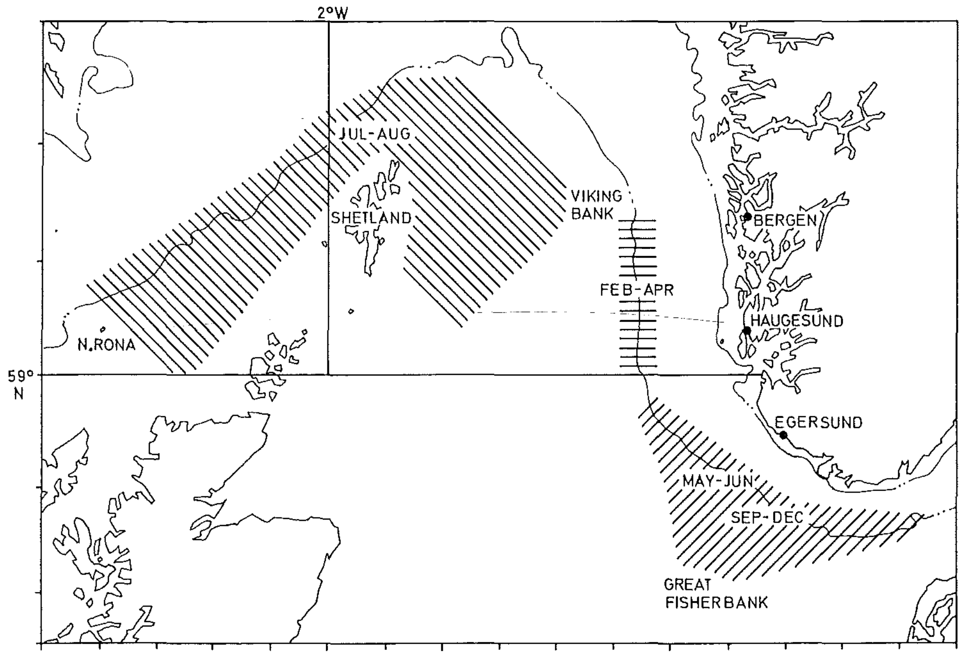

Figure 7. Main fishing grounds of Norwegian purse seiners by season.

As in the North Sea, most of the Western mackerel landed by trawlers prior to the 1960s was a by-catch from demersal fisheries. In the 1970s aimed trawling for mackerel was developed in both the Cornish area and the Celtic Sea. A dramatic expansion of the trawl fishery occurred with the arrival of large USSR pelagic trawlers, which increased the international catch in division VII from about 50000 t in 1969 to about 300000 t in 1976.

Up to 1976 purse seining for mackerel has been of relatively minor importance in the area west of the British Isles, apart from the area between Rona and Shetland mentioned in the discussion of the North Sea fishery. Since 1975, however, Scottish purse seiners have landed significant quantities of mackerel off Cornwall during the winter fishery and from late summer to autumn in division VIa.

STOCK ASSESSMENT AND MANAGEMENT

The mackerel spawning on both sides of the British Isles have been assessed as two separate stock units. Both stocks contribute to the fishery in the Shetland area from July to September, and the catch reported from ICES statistical division IVa during that period has been allocated to the two stocks according to recoveries of tagged fish. Catches from sub-areas VI, VII, and VIII are considered as Western mackerel, whereas the catches from division IIIa and the remainder of sub-area IV are regarded as being from the North Sea stock.

Assessment of the two stocks has been made on data from:

(a) catch statistics and biological sampling of the catch,
(b) catch per unit of effort,
(c) egg surveys,
(d) tagging.

NATIONAL INVESTIGATION AND SAMPLING PROGRAMMES

The North Sea mackerel catch has been sampled regularly for age composition by the Netherlands and Norway since the late 1950s and mid-1960s, respectively. The Netherlands has also collected catch and effort statistics from the spring trawl fishery. Norway has tagged mackerel regularly since 1969 and has conducted egg surveys since 1968. Apart from the international catch statistics, these sampling programmes have provided the main source of data for the assessment of the North Sea stock (Anon., 1974–1978).

Age compositions of the English mackerel catches from the Western area have been available since 1960, and of the Scottish catches since 1970. The Netherlands has provided age data from sub-area VI since 1967 and from sub-area VII since 1969, as well as some data from the Irish Sea (Anon., 1974). In recent years the English have collected catch and

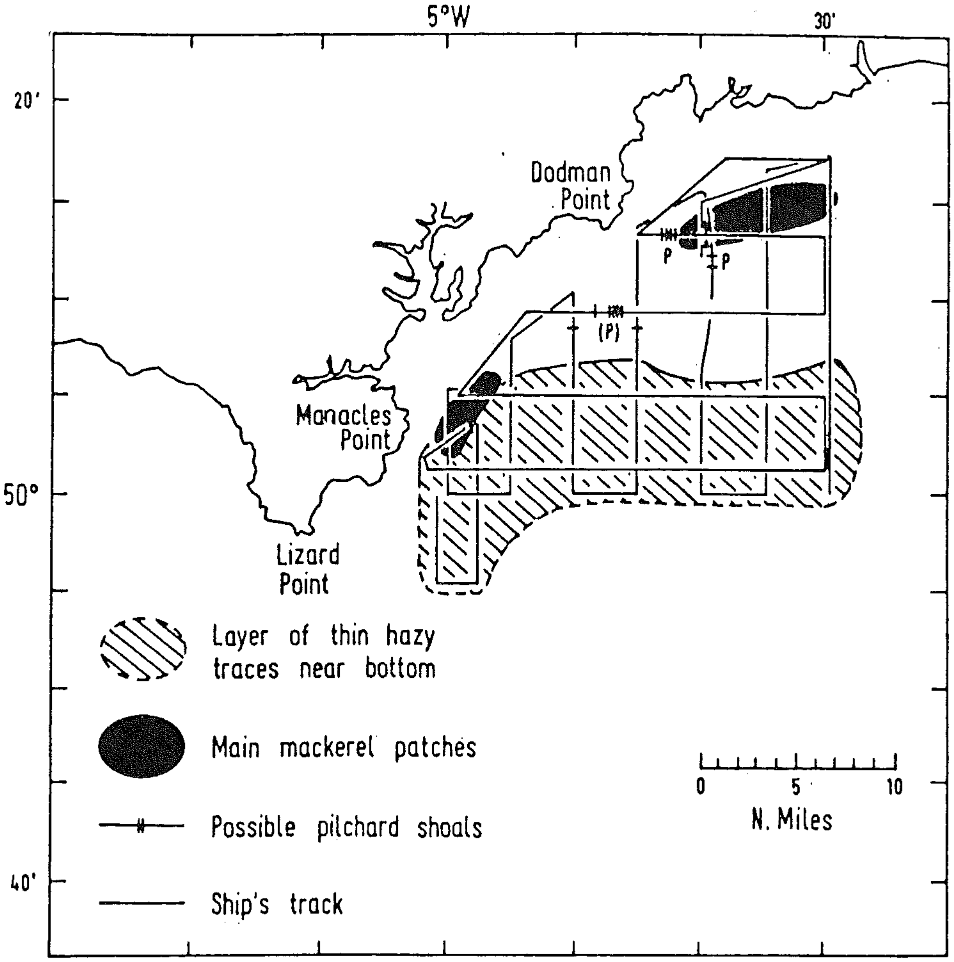

Figure 8. The distribution of both dense and diffuse mackerel shoals fished during December 1974 (Lockwood and Johnson, 1976).

effort statistics of their hook and line fishery. In 1977 an extensive egg survey was carried out on the spawning grounds west of the British Isles for abundance estimates of the Western spawning stock.

Since 1970 Norway has tagged and released mackerel in the Celtic Sea. The recaptures from these releases are from North Sea catches and have been used to identify the occurrence of the Western stock in the North Sea. Under special conditions these data may also be used for abundance estimates of the Western stock.

CATCH IN NUMBERS BY AGE

Catch in numbers by age is available for the North Sea stock from 1966 and from the Western stock since 1972. In Table 8a and b are given the respective catch figures for the years 1972–1977. The catches in division IVa of the North Sea are allocated to the North Sea and Western stocks using the proportions given in Table 17 (Hamre, 1978; Anon., 1978).

CATCH PER UNIT OF EFFORT

The Netherlands has collected catch and effort data from its trawl fishery in the North Sea since 1959, and the results from this investigation yielded the first consistent information on the declining North Sea mackerel stock in the 1960s (Postuma, 1972). Figure 9 shows the Dutch catch per unit of effort indices compared with VPA estimates of the stock in the years 1964–1970 using data from tagging as input of terminal N (Hamre, 1970). The two estimates agree very closely with respect to the trend in the stock development in the late 1960s. In more recent years, data on catch and effort statistics have been

Table 8a. North Sea mackerel stock. Catch in number with fishing mortality rates and stock sizes as derived from cohort analysis ($M = 0{\cdot}15$), 1972–1978. (Anon., 1978)

	Year class	1972	1973	1974	1975	1976	1977	1978
Catch in number (10^6)	Pre-1969	105·6	169·3	98·0	89·7	73·9	74·6	–
	1969	162·6	280·2	240·8	193·2	116·2	118·2	–
	1970	35·6	37·6	39·9	27·8	20·6	18·1	–
	1971	2·6	12·1	23·6	42·4	46·2	42·4	–
	1972	–	4·5	18·7	16·2	14·2	11·5	–
	1973	–	–	2·9	10·1	69·7	59·4	–
	1974	–	–	–	11·9	73·6	63·4	–
	1975	–	–	–	–	2·7	23·8	–
	1976	–	–	–	–	–	1·3	–
	Total	306·4	503·7	423·9	391·1	417·1	415·7	–
Fishing mortality (F)	Pre-1969	0·084	0·177	0·140	0·174	0·200	0·300	–
	1969	0·074	0·166	0·199	0·230	0·199	0·300	–
	1970	0·104	0·144	0·212	0·212	0·227	0·300	–
	1971	0·005	0·026	0·062	0·144	0·219	0·300	–
	1972	–	0·030	0·061	0·193	0·244	0·300	–
	1973	–	–	0·006	0·026	0·233	0·300	–
	1974	–	–	–	0·028	0·231	0·300	–
	1975	–	–	–	–	0·018	0·200	–
	1976	–	–	–	–	–	0·009	–
$\bar{F} \geq 3$ years		0·078	0·168	0·164	0·199	0·211	0·300	–
Stock size, 1 Jan (10^6)	Pre-1969	1 418·3	1 123·3	809·8	606·1	438·4	308·8	196·9
	1969	2 467·1	1 972·6	1 437·9	1 014·2	693·7	489·3	312·0
	1970	389·6	302·3	225·3	156·9	109·3	74·9	47·8
	1971	586·3	502·2	421·0	340·5	253·7	175·5	111·9
	1972	–	162·6	135·8	99·5	70·6	47·6	30·4
	1973	–	–	502·8	430·1	360·8	245·9	156·8
	1974	–	–	–	459·3	384·2	262·4	167·3
	1975	–	–	–	–	166·8	141·0	99·4
	1976	–	–	–	–	–	(160·0)	136·5
	1977	–	–	–	–	–	–	(160·0)
	Total	4 861·9	4 063·0	3 532·6	3 106·6	2 477·5	1 905·4	1 419·0
Spawning stock (≥ 3 years) biomass (10^3 t)		1 471·5	1 295·2	1 098·5	839·3	799·3	657·5	469·4

available from the Dutch, English, and Scottish fisheries. The Dutch data refer to a herring-directed fishery and the Scottish data to the whitefish fishery in the North Sea in which mackerel are taken as by-catch. Figure 10 compares the calculated stock size for the North Sea on the basis of tagging with the Scottish and Dutch CPUE figures. There seems to be a reasonable correspondence in the different abundance estimates (Anon., 1978).

The English CPUE data are derived from the mackerel hand-line fishery off southwest England (division VIIe, f). Such data are available from November 1972. Integrated seasonal means (September–March) are listed in Table 9 in tonnes per 100 hook hours.

All CPUE data show a marked decline in abundance of both the North Sea and the Western stocks (Anon., 1978).

EGG SURVEYS

Abundance estimates of both the Western and the North Sea mackerel stocks have been obtained from egg surveys. The method is based on data on the total egg production, fecundity, and the sex ratio of the spawning stock. The number of female spawners is estimated by dividing the total egg production by the mean fecundity and raised, according to the sex ratio, to the total numbers of spawners.

For the Western stock, in 1977 the English carried out an extensive egg survey in the area west of the British Isles. The mackerel eggs were collected during six surveys in March–July 1977 in the Bay of Biscay, Celtic Sea, and west of Ireland (Lockwood, Coombs, and Guéguen, 1977a). The eggs were removed from plankton samples collected with a 30″ Lowestoft pattern TTN fitted with a 60 mesh/inch net. The net was towed at 5 knots from the surface to 100 m depth

Table 8b. Western mackerel stock. Catch in number with fishing mortality rates and stock sizes as derived from cohort analysis ($M = 0{\cdot}15$), 1972–1978. (Anon., 1978)

	Year class	1972	1973	1974	1975	1976	1977	1978
Catch in number (10^6)	Pre-1969	507·7	582·3	567·0	1 246·2	416·2	139·7	–
	1969	29·4	115·5	191·8	143·8	282·0	97·7	–
	1970	12·1	64·0	108·5	192·2	117·5	77·4	–
	1971	12·4	49·4	123·5	306·3	276·4	123·9	–
	1972	1·6	33·8	24·3	94·5	170·3	46·7	–
	1973	–	–	87·0	104·0	322·3	160·2	–
	1974	–	–	1·3	52·5	184·9	148·4	–
	1975	–	–	–	1·0	279·5	276·1	–
	1976	–	–	–	–	34·1	135·8	–
	1977	–	–	–	–	–	2·0	–
	Total	563·2	845·0	1 103·4	2 140·5	2 083·2	1 207·9	–
Fishing mortality (F)	Pre-1969	0·068	0·098	0·124	0·410	0·219	0·100	–
	1969	0·009	0·041	0·085	0·081	0·213	0·100	–
	1970	0·005	0·031	0·064	0·145	0·117	0·100	–
	1971	0·003	0·015	0·044	0·138	0·168	0·100	–
	1972	–	0·025	0·022	0·104	0·262	0·100	–
	1973	–	–	0·027	0·039	0·153	0·100	–
	1974	–	–	–	0·022	0·097	0·100	–
	1975	–	–	–	–	0·042	0·050	–
	1976	–	–	–	–	–	0·037	–
	1977	–	–	–	–	–	–	–
$\bar{F} \geq 3$ years		0·050	0·071	0·088	0·223	0·184	0·100	–
Stock size, 1 Jan (10^6)	Pre-1969	8 368·0	6 731·4	5 253·6	3 995·8	2 283·0	1 578·9	1 229·6
	1969	3 590·0	3 062·6	2 528·9	1 998·7	1 586·9	1 104·2	860·0
	1970	2 658·6	2 277·1	1 900·5	1 535·1	1 143·0	874·8	681·3
	1971	4 280·0	3 672·4	3 115·0	2 566·5	1 924·9	1 400·3	1 090·6
	1972	–	1 454·0	1 220·1	1 027·6	796·8	527·8	411·1
	1973	–	–	3 532·5	2 959·8	2 451·0	1 810·6	1 410·1
	1974	–	–	–	2 552·2	2 148·0	1 677·2	1 306·2
	1975	–	–	–	–	7 379·9	6 092·6	4 988·2
	1976	–	–	–	–	–	(4 000·0)	3 317·8
	1977	–	–	–	–	–	–	(1 500·0)
	Total	18 896·6	17 197·5	17 550·6	16 635·7	19 713·5	19 066·4	16 794·9
Spawning stock ($\geq$ 3 years) biomass (10^3 t)		3 420·9	3 651·1	4 061·7	3 913·0	3 532·1	3 212·1	3 814·5

(or 2 m above the seabed) and back to the surface.

The eggs were ascribed to six developmental stages (Lockwood, Nichols, and Coombs, 1977b). For stock-size estimation, only stage I eggs were used. The numbers at this stage in the sample were raised first to an estimate of the numbers of eggs per m^2 and then corrected to numbers per m^2 per day using observed sea temperature data and a stage-duration correction factor (Lockwood et al., 1977b). To raise the observed numbers per m^2 for the total area, the survey area was divided into eight blocks. The standing stock of stage I eggs per cruise was the sum of the estimates for each of the eight blocks. The estimates of daily egg production in May and June were checked by contouring logarithms of number plus 1 below m^2 per day. The areas within each contour interval were converted to total daily egg production using the geometric mean of adjacent contours. This comparison indicated that the estimates were not markedly affected by using contouring instead of the arithmetic mean. The egg production curve was constructed by plotting the estimates of standing stock of eggs against time and drawing a curve by eye. The area under the curve was measured by planimetry.

The fecundity estimation was based on data collected by Macer (1976) and on additional fish caught along the edge of the continental shelf. The mean fecundity was estimated in different ways and ranged between 261 000 and 295 000. The mean fecundity was taken to be 300 000. The number of female spawners was estimated and raised to a total spawning stock of 8985×10^6 fish according to the sex ratio of 1·57 females to 1 male.

Another estimate based on the same data was made by transforming the daily egg production of stage I

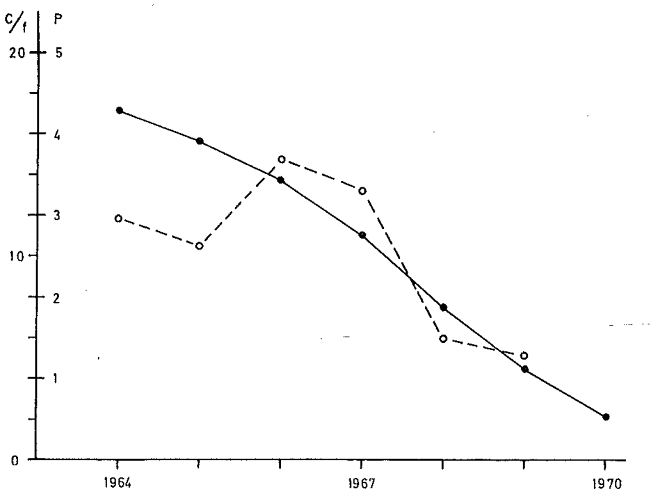

Figure 9. Stock abundance of mackerel in the northeastern North Sea by year. The broken curve shows the catch per unit of effort (C/f) in tonnes per 100 h fishing by a Dutch standard trawler. The solid curve shows the stock estimates in million tonnes based on a VPA estimate using results of Norwegian taggings in 1969–1970 as terminal value of N (Hamre, 1970).

eggs per station logarithmically (Anon., 1978). The mean of the transformed data was retransformed to the arithmetic mean. The daily egg production was calculated by multiplying this by the size of the investigated spawning area. These estimates were plotted against time (Fig. 11) and the total egg production estimated by measuring the area beneath the observations linked by straight lines. Additional data on fecundity gave a mean fecundity estimation for the spawning females as 282 530 eggs. The spawning stock was estimated as 9346×10^6 fish. This stock abundance estimate (10 000 million) divided among year classes was used to back-calculate stock strength and mortality for the years 1972–1977 using $M = 0{\cdot}15$. The results are shown in Table 8b (Anon., 1978; Lockwood, 1977, personal communication).

For the North Sea stock a Norwegian sampling programme for mackerel eggs in the North Sea and the Skagerrak has been carried out since 1968 (Iversen, 1973; 1977). In the first four years the area north of 57°N was investigated. In later years the area north of 56°N (1973) and north of 55°N (since 1974) has been surveyed. Plankton samples were collected with

Table 9. Integrated seasonal means (t/100 hook h) in division VIIe, f, September–March, 1972–1976

1972/1973	1973/1974	1974/1975	1975/1976
0·27	0·23	0·16	0·10

a Juday net, diameter 80 cm and mesh size 500 μ. In addition, four Clarke-Bumpus plankton samplers (mesh size 500 μ) were used at different depths to give the vertical distribution of the mackerel eggs. As a result of these investigations the sampling design was changed in 1973 to four Clarke-Bumpus samplers at 0, 5, 10, and 15 m depths. The samplers are towed for 10 minutes at a speed of ca. 3 knots. The mackerel eggs are grouped into two stages of development, those with and those without visible embryos. According to the temperature in the spawning area and experiments carried out by Danielsen and Iversen (1977), the eggs without visible embryos are less than two days old. These eggs, which have an average age of one day, were used to estimate spawning stock size. The numbers of these eggs per m² were estimated for each station. Smoothed values were plotted on charts and isolines drawn. The area within each isoline was measured and raised by the isoline value to the total amount of eggs.

Bakken, Bjørke, and Afonso (1977) have suggested that the spawning lasts for 30 days and that the spawning activity is more or less constant throughout this period (Fig. 4). By including data from Johnson and Dawson (1975) it seems that roughly 45% of the mackerel eggs are spawned north and 55% south of 57°N. The total egg production has been estimated for each of the years 1968–1975 (Iversen, 1977).

There is no published data on fecundity of North Sea mackerel. The mean fecundity is therefore based on data from the Western stock (Macer, 1976). The numbers of female spawners were raised according to the sex ratio of 1 female to 1 male. The results are plotted in Figure 12. A more southerly or northerly spawning than usual will affect the estimates of the years with the lesser coverage of the spawning area. In the later years with fuller coverage of the spawning area, the estimates fit well with estimates based on tagging experiments (Fig. 12).

TAGGING

The tagging programme

After several test experiments on tagging methods carried out from 1965 to 1969, an annual tagging programme for mackerel was initiated by Norway in the autumn of 1969. The programme consists of releasing internally tagged fish in July/August in the eastern North Sea and Skagerrak spawning area and in May in the Celtic Sea. In the North Sea the fish are tagged from catches taken by trolling and in the Celtic Sea by jig. The tagged fish are measured and samples of the catch are taken regularly to establish age-length keys.

The tags are recovered on magnets installed in the

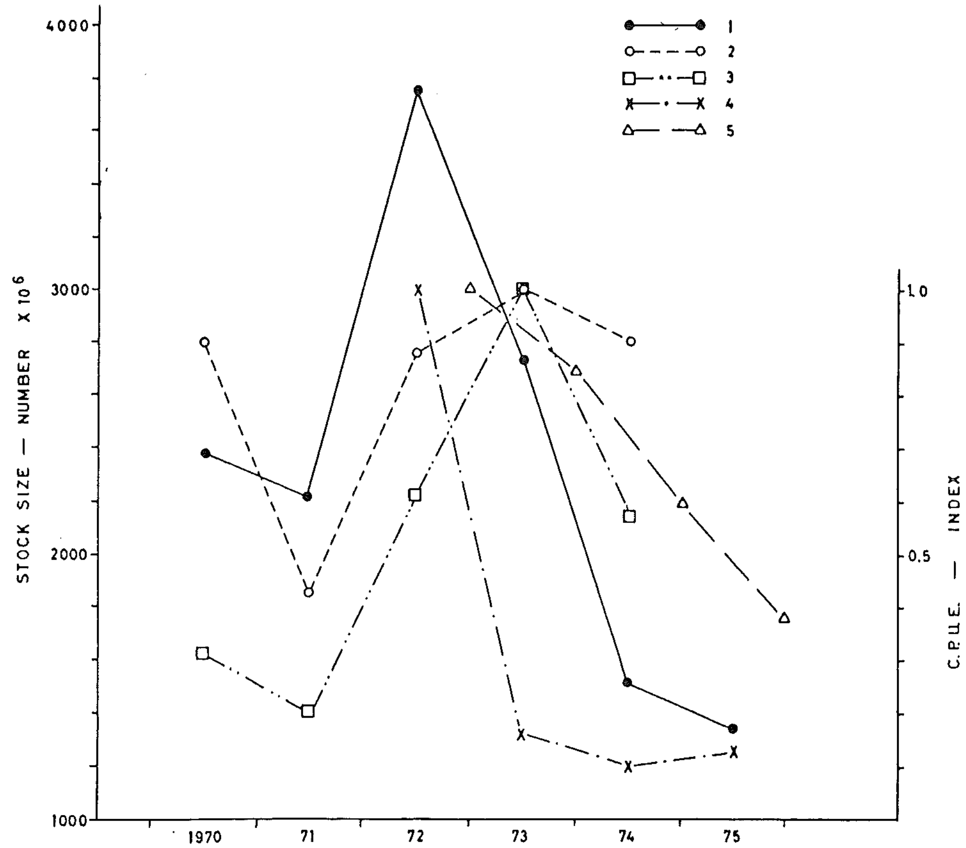

Figure 10. Mackerel stock size in the North Sea as derived from tagging compared with measures of catch per unit of effort from various mackerel fisheries (Anon., 1978). 1) Stock size (1969 and older year classes), 1 September. 2) CPUE, Scottish trawl fishery (Orkney–Shetland), July–September. 3) CPUE, Scottish trawl fishery (Cape Butt). 4) CPUE, Dutch trawl fishery (North Sea). 5) CPUE, English hand-line fishery (division VII e,f), September–March.

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. The number of tags returned by year class and the corresponding catch are given in Tables 10 and 11 for the North Sea and the Western stock respectively. The year classes are divided into two groups, the 1969 year class and the older year classes. For the years 1970 to 1975 the returns are related to two areas: the Shetland area (Sh), covering the fishery from July to mid-September, and the eastern part of sub-area IVa (NS), which mainly refers to the autumn fishery (after mid-September). For the last two years such a division has not been made (Anon., 1978).

The recoveries reported constitute only a fraction of the total catch, but the corresponding catch effectively screened for tags is also reported. Given the total international catch in the distribution area of the tagged fish, the total number of tagged mackerel caught can be calculated. The raised number of returns from the North Sea tagging is shown in Table 12. The area considered as the distribution area of the tagged fish, in addition to division IVa includes IIa, IIIa, and IVb, as well as the northern part of VIa where some of the Norwegian catch was taken. The data on total international catch in number given in Table 12 are mainly obtained from ICES Mackerel Working Group reports. The raised numbers of tag returns given in Table 12 differ slightly from those given in the last Working Group report (Anon., 1978). The difference is, however, so slight that the results are not affected.

Theories of data compilation

From tagging one can obtain estimates of stock size, recruitment, and mortality rates. Tagging data may further be used for migration studies and to estimate the contribution of separate stocks to a mixed fishery.

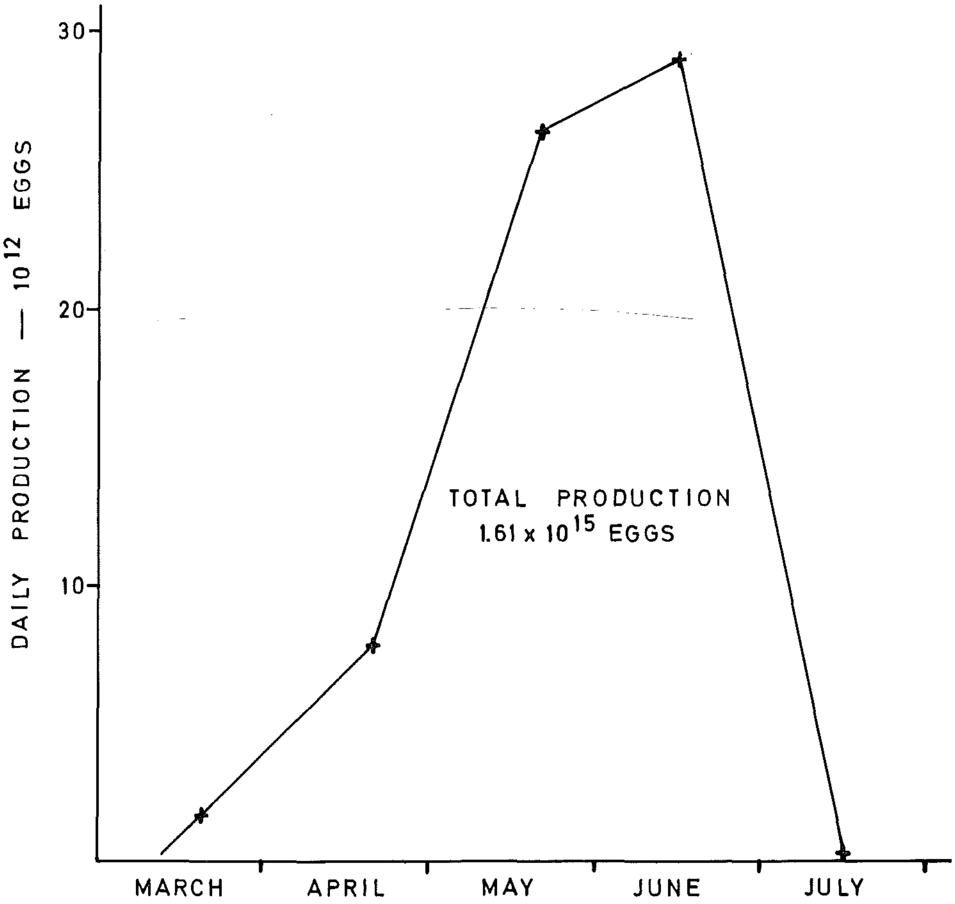

Figure 11. Egg production, number per m² per day. Western mackerel stock (Anon., 1978).

Table 10. Tag recoveries from the Shetland area (Sh) and the northeastern North Sea (NS) in Norwegian catches as number $\times 10^{-6}$ effectively screened for tags (C_j). Tagged in the North Sea

Year class	Year of release	n	Year of recapture 1969 NS	1970 Sh	1970 NS	1971 Sh	1971 NS	1972 Sh	1972 NS	1973 Sh	1973 NS	1974 Sh	1974 NS	1975 Sh	1975 NS	1976	1977
Pre-1969	1969	4 187	547	16	198	50	6	4	5	22	2	8	9	2	5	6	3
	1970	2 420	–	–	443	30	10	6	19	22	26	13	15	2	14	12	7
	1971	2 450	–	–	–	–	41	21	36	35	52	23	48	6	36	24	20
	1972	2 126	–	–	–	–	–	–	44	33	80	20	68	5	44	33	33
	1973	1 518	–	–	–	–	–	–	–	–	106	18	80	8	62	37	30
	1974	1 344	–	–	–	–	–	–	–	–	–	–	121	4	47	23	33
	1975	1 048	–	–	–	–	–	–	–	–	–	–	–	–	100	20	39
	1976	304	–	–	–	–	–	–	–	–	–	–	–	–	–	11	13
		C_j	307·2	41·5	212·7	170·5	8·6	60·2	32·3	204·6	62·9	114·7	30·7	80·5	36·0	53·8	33·5
1969	1970	1 085	–	–	33	4	9	3	11	9	21	4	21	2	17	7	12
	1971	6 900	–	–	–	–	113	36	109	107	233	64	170	16	137	85	72
	1972	9 447	–	–	–	–	–	–	132	108	401	92	383	29	284	163	160
	1973	4 642	–	–	–	–	–	–	–	–	301	34	271	22	216	92	96
	1974	2 740	–	–	–	–	–	–	–	–	–	–	265	7	132	58	77
	1975	4 716	–	–	–	–	–	–	–	–	–	–	–	–	451	123	152
	1976	996	–	–	–	–	–	–	–	–	–	–	–	–	–	32	36
		C_j	–	–	39·6	7·5	24·3	17·8	52·3	51·9	120·3	75.2	112·3	18·2	97·7	93·2	65·6

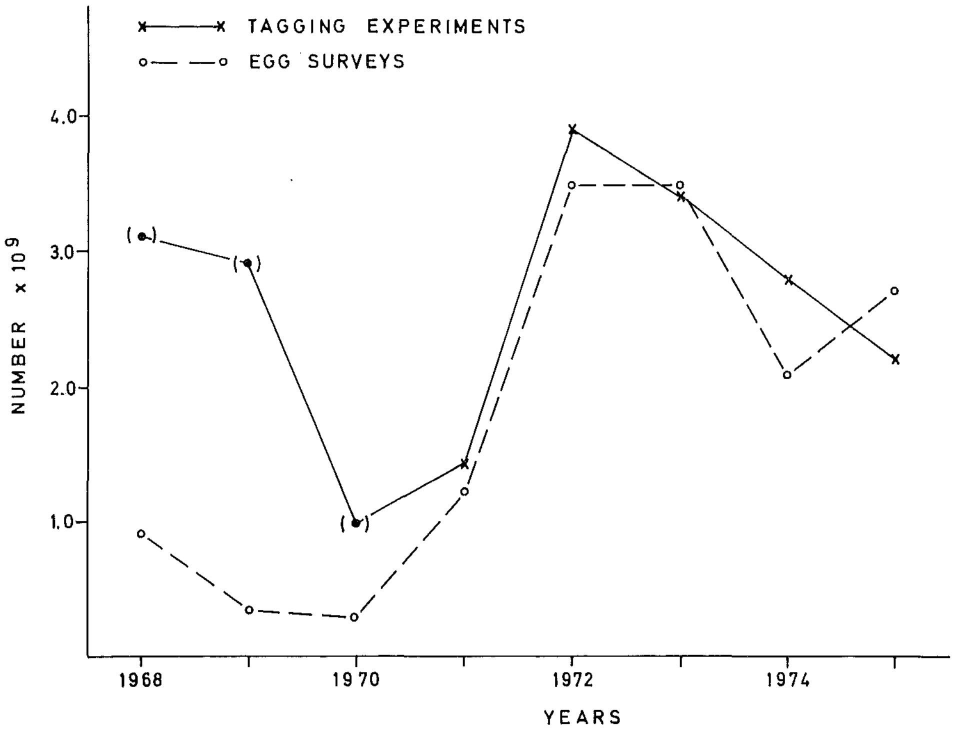

Figure 12. Estimated spawning stock size of North Sea mackerel based on tagging experiments and egg surveys.

Petersen (1896) introduced the method of using tagged fish to estimate population size (N), with the equation

$$N = (mC)/r \tag{1}$$

where m denotes the number of surviving tagged fish, C the catch, and r the corresponding recoveries. This simple stock estimate, termed the single census estimate (Ricker, 1975), is the basic element in all the mathematical models used in data compilation of composite tagging programmes.

The mackerel tagging programme yields recovery data from successive releases, the time between the releases being one year, starting from May for the

Table 11. Tag recoveries from the Shetland area (Sh) and the northern North Sea (NS) in Norwegian catches as number $\times 10^{-6}$ effectively screened for tags (C_j). Tagged in the Celtic Sea

			Year of recapture													
Year class	Year of release	n	1970 Sh	1970 NS	1971 Sh	1971 NS	1972 Sh	1972 NS	1973 Sh	1973 NS	1974 Sh	1974 NS	1975 Sh	1975 NS	1976	1977
Pre-1969	1970	4 540	0	1	0	0	2	1	15	13	17	10	7	17	19	12
	1971	5 000	–	–	50	5	14	8	52	22	31	13	5	11	14	15
	1972	5 086	–	–	–	–	19	9	48	32	40	24	15	16	20	13
	1973	3 979	–	–	–	–	–	–	11	10	26	15	5	11	13	8
	1974	6 900	–	–	–	–	–	–	–	–	73	42	49	61	34	30
	1975	6 938	–	–	–	–	–	–	–	–	–	–	42	40	47	27
	1976	5 652	–	–	–	–	–	–	–	–	–	–	–	–	27	18
		C_j	41·5	212·7	170·5	8·6	60·2	32·3	204·6	62·9	114·7	30·7	80·5	36·0	53·8	33·5
1969	1973	3 232	–	–	–	–	–	–	3	2	12	8	9	14	11	6
	1974	2 246	–	–	–	–	–	–	–	–	20	12	15	24	16	13
	1975	861	–	–	–	–	–	–	–	–	–	–	3	3	5	3
	1976	–	–	–	–	–	–	–	–	–	–	–	–	–	5	2
		C_j	–	–	–	–	–	–	51·9	120·3	75·2	112·3	18·2	97·7	93·2	65·6

Table 12. Tag recoveries from the Shetland area and the northeastern North Sea raised to total catch as number $\times 10^{-6}$ (C_T). Tagged in the North Sea

Year of release	Within-season recapture	Year of recapture 1970	1971	1972	1973	1974	1975	1976	1977
Pre-1969 year class									
1969	1 250	466	116	23	36	30	13	13	8
1970	917	–	88	65	82	50	30	26	19
1971	92	–	–	146	148	128	78	51	54
1972	115	–	–	–	197	161	90	70	90
1973	200	–	–	–	–	173	130	79	82
1974	219	–	–	–	–	–	94	49	90
1975	182	–	–	–	–	–	–	43	106
C_T		614·8	392·1	231·9	412·4	260·1	231·0	114·5	91·1
1969 year class									
1970	66	–	42	32	51	46	35	18	30
1971	364	–	–	345	579	427	283	217	179
1972	304	–	–	–	886	848	578	416	398
1973	548	–	–	–	–	528	439	235	239
1974	448	–	–	–	–	–	255	148	192
1975	821	–	–	–	–	–	–	314	379
C_T		–	102·4	262·0	293·9	352·6	216·5	237·3	163·2

Celtic Sea and from August for the North Sea releases. The recaptures are obtained from catches mainly taken from August to October, i.e. immediately after the spawning season. The data from such a programme may be set out in a triangular array as seen in Table 13.

From such an array several Petersen-type stock size estimates can be obtained. The Petersen estimate gives the stock size at the time when m surviving tagged fish are mixed in the population and presupposes that there is no recruitment in the period between marking and capture. When the tagged fish are grouped in year classes which are fully recruited to the catchable stock there will be no time limitation on the sampling period. Using Equation (1) the stock size at the beginning of the period i is:

$$N_i = \frac{s_i\, m_i \sum_{j=i}^{j} C_j}{\sum_{j=i}^{j} r_{ij}} \qquad (2)$$

Summing r and C from $j = i+1$ to j all the within-season recoveries are excluded from the estimate. This may avoid error due to incomplete mixing of tagged fish in the population.

Ricker (1948) showed that the survival rate could be estimated from two successive Petersen censuses. For fully recruited year classes a similar form of multiple census can be developed. By definition, the survival (S) is: $S_i = N_{i+1}/N_i$.

From Equation (2) we have:

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

Summing r from $j = i+1$ to j all the within-season recoveries are excluded.

Equation (3) does not include the catch, and is consequently not influenced by the source of error

Table 13. Triangular array of recovery data from successive releases; m = number released, r = number recovered in the sample or catch C, and s = survival factor. The indices i and j denote successive intervals of releases and recoveries respectively

	$ij =$	0	1	2	3	4	j
$s_0\ m_0$	0	r_{00}	r_{01}	r_{02}	r_{03}	r_{04}	r_{0j}
$s_1\ m_1$	1		r_{11}	r_{12}	r_{13}	r_{14}	r_{1j}
$s_2\ m_2$	2			r_{22}	r_{23}	r_{24}	r_{2j}
$r_3\ m_3$	3				r_{33}	r_{34}	r_{3j}
$s_4\ m_4$	4					r_{44}	r_{4i}
$s_j\ m_i$	i						r_{ij}
Catch:		C_0	C_1	C_2	C_3	C_4	C_j

of non-reported recaptured tags. The formula includes s but if the variation in tagging survival is small the fraction s_{i+1}/s_i approaches unity and may be neglected. Standardizing the field work in order to reduce possible annual variation in s has therefore been an important task in the tagging programme (Hamre, 1978).

Fisher and Ford (1947) have described a method of using a recapture diagram of successive releases for estimating the abundance of an insect population, assuming a constant death rate and a negligible mortality due to the tagging operation. This method has been used in an adjusted form to estimate the size of the North Sea mackerel stock (Hamre, 1978).

In principle this method is also based on a Petersen estimate of the stock size using Equation (1). The precision in a Petersen estimate is proportional to the number of recaptured fish, and the aim of the method is to obtain a weighted estimate of the population size, including recoveries from all the releases prior to the time of sampling.

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 including recoveries from all the previous releases. Assuming a constant s, a single census estimate of the stock size N at time j may be expressed as:

$$N_j = \frac{C_j\, s \sum_{i=0}^{i=j} m_{ij}}{\sum_{i=0}^{i=j} r_{ij}} \qquad (4)$$

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 time j, including all the previous releases.

Fisher and Ford (1947) estimated the number of surviving tagged animals at each time interval of sampling by selecting a constant mortality rate according to the goodness of fit of the observed recoveries to the corresponding calculated expectation.

In an exploited fish population the mortality rate changes with the rate of fishing and thus this method cannot be applied. However, an estimate of the number of surviving tagged fish at any time interval prior to j is obtainable using Equation (3), provided the total mortality rate, measured between the releases in the interval i to $(i+1)$, is valid for all the previous releases.

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

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

Table 14a. Survival estimates of mackerel tagged in the North Sea. S_i denotes estimates according to Equation (3); $(S_i)_R$ denotes estimates obtained by Robson's method. Recoveries from the first $1^1/_2$ years are excluded.

Year class	Year of release	n	S_i	$(S_i)_R$
Pre-1969	1969	4 187	0·40	0·40
	1970	2 420	0·46	0·40
	1971	2 450	0·67	0·68
	1972	2 126	0·72	0·60
	1973	1 518	1·13	1·09
	1974	1 344	0·74	0·74
	1975	1 048	0·87	0·67
	1976	304	–	–
1969	1970	1 085	0·66	0·66
	1971	6 900	0·75	0·75
	1972	9 447	0·75	0·72
	1973	4 642	0·92	0·91
	1974	2 740	0·84	0·83
	1975	4 716	0·89	0·84
	1976	996	–	–

Table 14b. Survival estimates of mackerel tagged in the Celtic Sea (see text for Table 14a)

Year class	Year of release	n	S_i	$(S_i)_R$
Pre-1969 and 1969	1970	4 540	0·67	0·67
	1971	5 000	0·80	0·83
	1972	5 086	1·31	1·33
	1973	7 211	0·42	0·42
	1974	9 146	0·83	1·04
	1975	7 466	1·31	1·53
	1976	6 513	–	–

and the total m_{ij} at time j:

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

As for Equation (3) the within-season recaptures may be excluded in Equation (4) by summing m from $i = 0$ to $i = j-1$.

Recalling that the survival can be expressed as the fraction of two consecutive Petersen stock estimates ($S_i = N_{i+1}/N_i$) an extended formula for the survival is available, making use of all the recoveries from releases prior to the time j. In this N_{i+1} is estimated according to Equation (2), whereas N_i is estimated according to Equation (4) including all the recoveries from the releases prior to $i = j$, or $i = j-1$ omitting first-year recoveries. This is the same model as that developed by Robson in 1963, and in a more general form by Seber in 1972. Estimates of survival by using Equation (3) and Robson's method are given in Tables 14a and 14b. It is seen that the estimates ob-

Table 15. VPA of mackerel tagged in the North Sea. $M = 0{\cdot}13$

	j:			1969			1970			1971			1972			1973		
	i:	*m*	*s*	*s m*	*r*	*F*	*s m*	*r*	*F*	*s m*	*r*	*F*	*s m*	*r*	*F*	*s m*	*r*	*F*
1969	1970	1 085	0·618				671	66	0·107	564	42	0·085	455	32	0·081	368	51	0·165
year	1971	6 900	0·638							4 399	364	0·089	3 770	345	0·106	2 977	579	0·241
class	1972	9 447	0·696										6 577	304	0·049	5 869	886	0·182
	1973	4 642	0·741													3 442	548	0·179

				1974			1975			1976			1977		
		m	*s*	*s m*	*r*	*F*	*s m*	*r*	*F*	*s m*	*r*	*F*	*s m*	*r*	*F*
1969	1970	1 085	0·618	274	46	0·204	196	35	0·218	139	18	0·154	104	30	0·38
year	1971	6 900	0·638	2 054	427	0·260	1 391	283	0·253	948	217	0·290	623	179	0·38
class	1972	9 447	0·696	4 297	848	0·245	2 954	578	0·243	2 035	416	0·255	1 385	398	0·38
	1973	4 642	0·741	2 695	528	0·243	1 856	439	0·301	1 206	235	0·242	832	239	0·38
	1974	2 740	0·688	1 884	448	0·281	1 333	255	0·237	924	148	0·194	668	192	0·38
	1975	4 716	0·598				2 818	821	0·357	1 847	314	0·207	1 319	379	0·38

				1969			1970			1971			1972			1973		
		m	*s*	*s m*	*r*	*F*	*s m*	*r*	*F*	*s m*	*r*	*F*	*s m*	*r*	*F*	*s m*	*r*	*F*
Pre-1969	1969	4 187	0·544	2 279	1 250	0·830	931	466	0·797	369	116	0·425	212	23	0·128	164	36	0·277
year	1970	2 420	0·668				1 617	917	0·875	631	88	0·167	469	65	0·165	349	82	0·299
class	1971	2 450	0·522							1 280	92	0·077	1 110	146	0·156	834	148	0·217
	1972	2 126	0·651										1 385	115	0·090	1 187	197	0·202
	1973	1 518	0·760													1 153	200	0·197

				1974			1975			1976			1977		
		m	*s*	*s m*	*r*	*F*	*s m*	*r*	*F*	*s m*	*r*	*F*	*s m*	*r*	*F*
Pre-1969	1969	4 187	0·544	109	30	0·361	67	13	0·242	46	13	0·373	28	8	0·38
year	1970	2 420	0·668	227	50	0·277	151	30	0·246	104	26	0·322	66	19	0·38
class	1971	2 450	0·522	589	128	0·273	393	78	0·246	270	51	0·233	188	54	0·38
	1972	2 126	0·651	852	161	0·233	592	90	0·183	433	70	0·196	313	90	0·38
	1973	1 518	0·760	887	173	0·242	612	130	0·266	411	79	0·237	285	82	0·38
	1974	1 344	0·621	835	219	0·315	570	94	0·200	410	49	0·141	312	90	0·38
	1975	1 048	0·655				687	182	0·319	468	43	0·107	369	106	0·38

tained by applying the different models do not differ significantly when the number of recoveries is as large as in the present study.

From 1973 onwards the mortality estimates derived from the between-release estimates are not reliable (Table 12), perhaps owing in part to variation in tagging survivals (s) and in part to non-random mixing of the tagged fish. The various releases have been subject to different fishing mortality rates (Table 15). It should also be noted that this method measures the total mortality in a batch of tagged fish in the first year after release. When the tagging takes place outside the main area of fishing the mortality estimate in the tagged population may not reflect the overall mortality in the untagged one.

A weighted estimate of the recruitment (R) similar to that of Equation (3) can be obtained from the basic formula developed by Bailey (1951):

$$R_j = \frac{e_{j+1}\, C_{j+1} \sum_{i=0}^{i=j} r_{ij}}{e_j\, C_j \sum_{i=0}^{i=j} r_{i\,(j+1)}} \qquad (5)$$

where e is the coefficient of magnet efficiency.

Equation (5) provides an estimate of the recruitment for the period between sampling and is independent of the number of surviving tagged fish. It is also independent of any systematical error in the magnet efficiency tests. Summing r from $i = 0$ to $(j-1)$, the within-season recaptures are excluded (Hamre, 1978).

The survival estimates referred to above are based on recaptures from successive releases of tagged fish in a common unit of catch. This type of estimate is valid when reporting is incomplete since the models are independent of the catch figures and provide the quickest way of obtaining a consistent estimate of mortality based on tagging. If the magnitude of the natural mortality (M) is available from other data sources, the stock size (N) can be estimated according to the catch equation:

$$N = (CZ)/F\,[1-\exp(-Z)] \qquad (6)$$

This procedure does not require an estimate of the tagging survival s, and has therefore been preferred in assessing the state of the North Sea mackerel stock based on tagging (Hamre, 1978; Anon., 1977).

Another way of estimating the mortality rate from tagging data is based on the relation between the rate of recovery and the rate of fishing. In this type of estimate the mortality is estimated on the basis of the total number of recaptures per time interval over a series of consecutive intervals. For this method to be valid it is therefore necessary that all tagged fish be reported when caught, or that the total number of recoveries can be estimated from available data (Table 12). (A fraction may be used under special conditions). The procedure used so far is based on the Beverton and Holt catch equation, run backwards. Plotting the logarithms of the number of recaptures against time it can be shown that the plots will fall in a straight line if the total mortality (Z) has been constant during the period of study. The slope of this line provides an estimate of Z, and the intercept of the log (r)-axis an estimate of M if the initial number of surviving tagged fish ($s\,m$) is known or vice versa.

In an exploited fish population the mortality varies with the rate of fishing, and the limitation of this method is that the condition of a constant Z is seldom fulfilled in a fishery. Using the Beverton and Holt catch equation backwards and stepwise, fishing mortality and population size can, however, be estimated when Z varies, provided an estimate of M is available. This is the Virtual Population Analysis (VPA), and the procedure involved is expressed by two equations:

$$C_t = \frac{F_t\,N_t}{Z_t}\,[1-\exp(-Z_t)]$$

$$N_{t+1} = N_t \exp(-Z_t)$$

where $Z = F+M$.

The common input data in the VPA is the catch by year class and year, natural mortality (M), and terminal population size (N_s) or terminal fishing mortality (F_s). Fishing mortality (F_t) and population size (N_t) are back-calculated by years (t).

Using the total recoveries from a batch of tagged fish as input data (Table 12), and assumed values of M and F_s, a VPA can be used to back-calculate prior fishing mortality F_j and surviving tagged fish $s_i\,m_{ij}$ for each batch of releases, regarding the tagged population as a unit stock and the yearly releases as cohorts of that stock. The initial $s_i\,m_i$ can thus be calculated, and given the number released, m_i, an estimate of s_i is obtained.

Assuming M to be constant and applying VPA runs on the recoveries from several releases which have passed through the fishery, a method of determining M is provided. The method requires long time series of recoveries which are now beginning to become available in the mackerel tagging programme. The compilation of such data is new, and a more detailed description of the procedures involved is therefore required.

There are in principle three different approaches to the solution of M by applying VPA on tag recoveries. The simplest is to select by trial VPA runs the M-value which best fits the corresponding estimates between releases obtained by Equation (3). This method has, however, turned out to be less satisfactory because of the low reliability of the latter type of estimates.

The other two approaches are founded on an analysis of the correlation between tagging survival s and the choice of M, and how this correlation is affected by (a) differences in generated fishing mortality, and (b) differences in number of executed steps in the VPA run, by comparing the most recent releases with those of earlier years. The type (a) approach is illustrated in Figure 13, which shows the estimated s-values as a function of M by applying VPA to seven releases in the years 1969 to 1972. The tagged fish are grouped by age, separating the strong 1969 year class from the older age groups. The VPA runs were started in 1977, with a terminal F of 0·35. Although none of the releases has yet passed through the fishery it can be shown that the interrelationship between the curves in Figure 13 is not changed significantly by reasonably small changes in the terminal F.

The different batches of tagged fish in Figure 13 have been subjected to different exploitation patterns. The 1969 release of older age groups was heavily exploited in 1969 and 1970, whereas the 1970 release of the older age groups was subjected to a high F in 1970 only. All the other releases were very moderately fished before 1973 (Table 15). This difference in exploitation pattern changes the slope of the curves, a high F tending to flatten out the curve, a low F making the s–M curves steep.

If M is assumed to be constant and s a random variate, the upper limit of M which can be accepted according to Figure 13 is 0·22. For higher M-values the s-value may exceed 100% for one of the releases, which is unrealistic. For an M of 0·22 the maximum

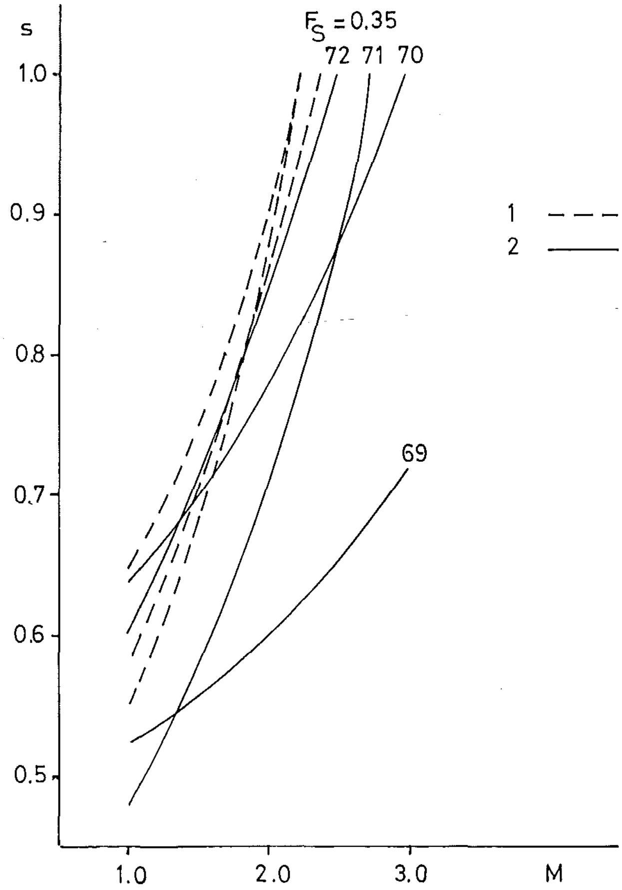

Figure 13. Tagging survival (s) as function of natural mortality (M) in VPA of recoveries of tagged mackerel.
1) 1969 year class released in 1970–1972.
2) Pre-1969 year class released in 1969–1972.
F_S = terminal fishing mortality in 1977.

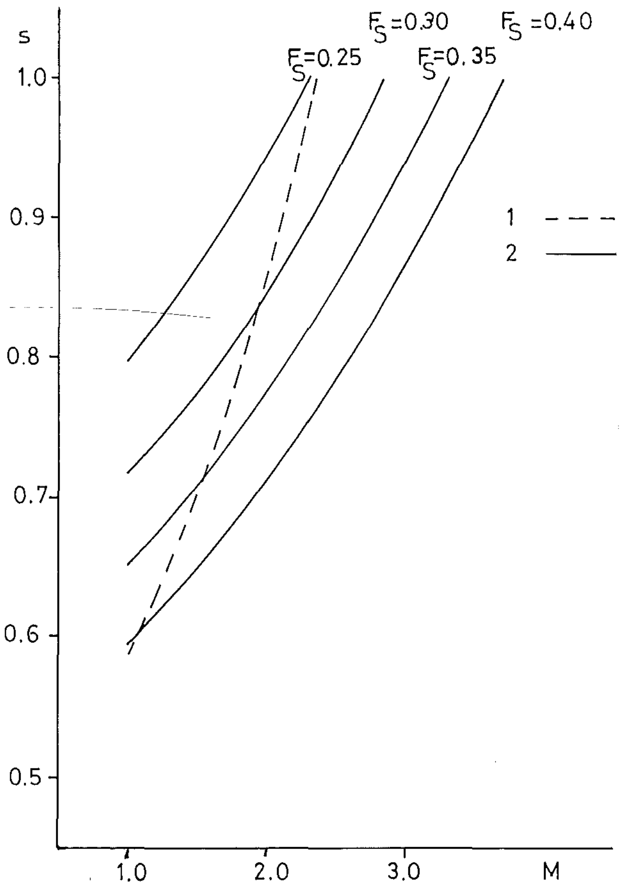

Figure 14. Tagging survival (s) as function of natural mortality (M) in VPA of recoveries of tagged mackerel.
1) Mean of the 3 hatched curves in Figure 13.
2) 1975 release.
F_S = terminal fishing mortality in 1977.

range of variation of s is 0·62 to 1·0. For lower M-values the range of s decreases and reaches a minimum for M of 0·13. This value of M is therefore the one which gives the best fit to all the data combined.

For M = 0·13, the s-values range from 0·54 to 0·73. It is seen that the 1969 and 1971 releases of fish older than the 1969 year class constitute one group with a common s of 0·54, whereas the other 5 releases show an average s of 0·68, ranging from 0·63 to 0·73. The reason for the low s-value in the former group is not known. Disregarding these two releases it seems reasonable to assume that the average s-value in the mackerel-tagging experiments in the North Sea is between 0·65 and 0·70. This is about 20% lower than that applied in previous assessments (Hamre, 1970; 1978).

To illustrate the determination of M by the type (b) solution the resultant curve of the 1970 to 1972 releases of the 1969 year class (the mean of the three hatched curves in Fig. 13) is compared with the computed s–M relationships of the 1975 release starting the VPA in 1977. Figure 14 shows the s–M relationship of the 1975 release for various terminal F-values in 1977 compared with that of the releases in the early 1970s. The estimated s in the 1975 release is, as the figure shows, very sensitive to the terminal F. If one chooses $F = 0{\cdot}35$ in 1977, the corresponding s–M values which best fit the 1970–1972 releases are those corresponding to the intercept between the resultant curve and the curve for $F_s = 0{\cdot}35$, i.e. 0·71 and 0·15 respectively. However, if one places more confidence in the M estimate of 0·13 derived from Figure 12, then Figure 13 suggests that the F in 1977 is slightly higher at about 0·38. Since a change in F_s to 0·38 does not change the s–M relationship in Figure 12 significantly, the best fit (minimum range of variation in s) is obtained for an M of 0·13.

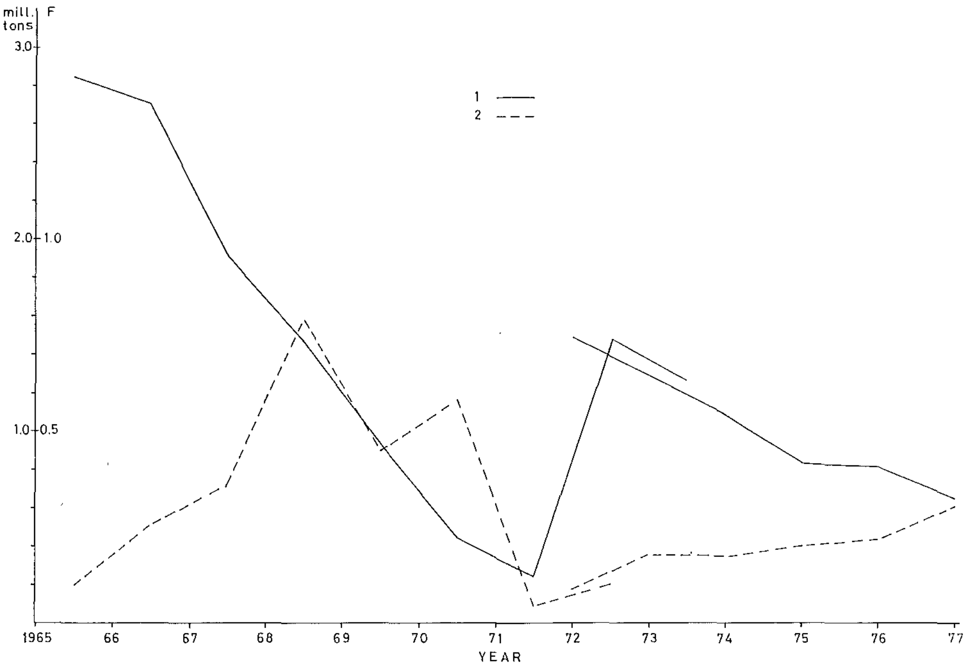

Figure 15. State of stock and exploitation of North Sea mackerel, 1965–1977. 1) adult stock biomass, 2) instantaneous fishing mortality (F). For further explanation see text.

Assuming an M equal to 0·13 for all the releases the state of stock and exploitation of the tagged population can now be assessed using the recoveries from all the releases. The inclusion of all the releases will increase the precision of the estimates, and contribute to increasing confidence in the results as reflecting the state of the untagged population.

It is reasonable to assume that tagged fish are not properly mixed with the previous releases in the first $1^1/_2$ years after release, and consequently not with the untagged population either. The procedure involved has therefore the aim of estimating the total number of surviving tagged fish for all releases which have been at liberty for more than $1^1/_2$ years. When one or more releases have passed through the fishery or have been at liberty for so long that a possible error in the choice of terminal F can be ignored, the number of surviving tagged fish can be back-calculated by applying a VPA to the number of recoveries, as in the usual way when input data are catches by age.

So far none of the releases has passed through the fishery and an estimate independent of the choice of terminal F cannot be made. The first releases have, however, been at liberty for so long that the effect of of an error in terminal F may be small. The process is therefore started by adding the recoveries from the 1969 and 1970 releases, and the surviving tagged fish (s m) are back-calculated from 1977 to 1973 by choosing a terminal F of 0·35. All the VPA calculations are made on a half-year basis, and the whole catch is considered as taken in the second half of the year. The back-calculated s m and the corresponding F are shown in the upper row of Table 16.

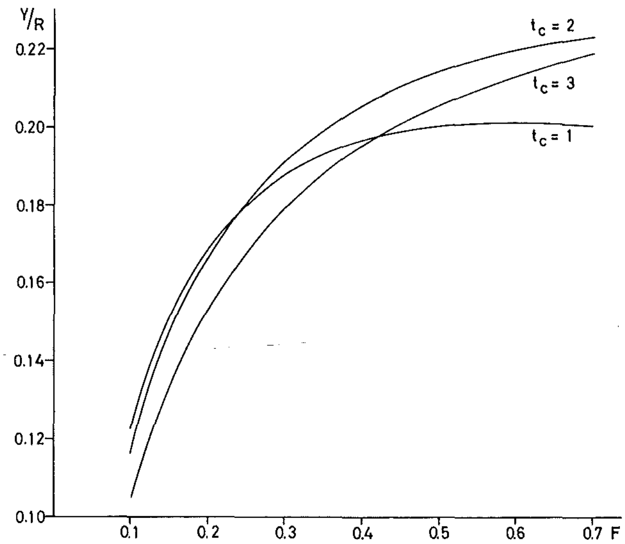

Figure 16. Yield per recruit (Y/R in kg) by fishing mortality (F) and age at first capture (t_c). $M = 0·20$ (Hamre and Ulltang, 1972).

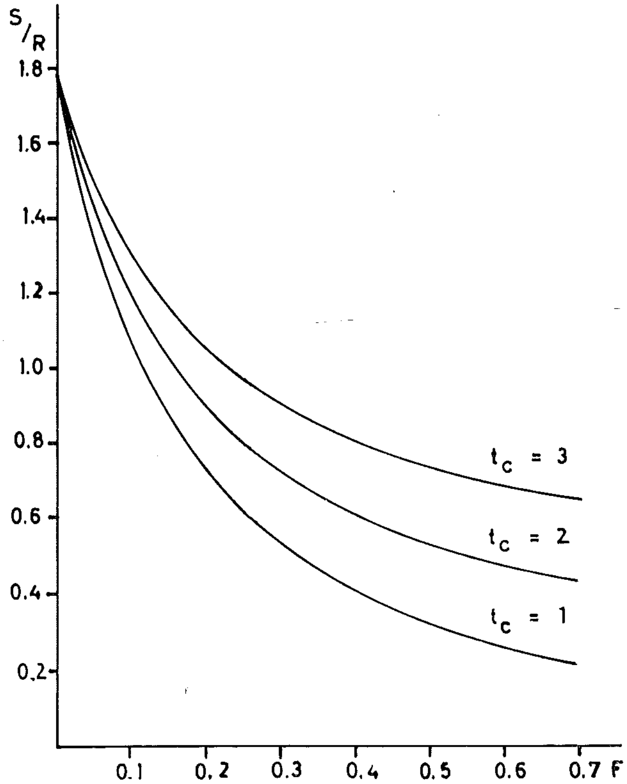

Figure 17. Spawning stock per recruit (S/R in kg) by fishing mortality (F) and age at first capture (t_c) (Hamre and Ulltang, 1972).

In 1973, the 1971 release had been at liberty for more than $1^1/_2$ years. This batch was added to the surviving tagged population by assuming that the 1971 release in 1973 was subject to the same F as that calculated for the 1969+1970 releases. Given F and r (0·23 and 727) the corresponding number of surviving tagged fish in 1973 was calculated (3650). This number, reduced by the total mortality in 1973, is the calculated number of surviving tagged fish in 1974 from the 1971 release (2547). Adding $s\ m$ from the 1969+1970 releases (592), the total number of surviving tagged fish in 1974 was found to be 3139. The corresponding number of recovered tags is 681. This gives an overall calculated fishing mortality in 1974 of 0·253. In 1974 the 1972 release was added to the surviving tagged population in the same way as the 1971 release in 1973 and the process of estimation was repeated. The result is given in Table 16. The state of the stock and the exploitation in 1977 is that 4524 tagged fish have yielded 1381 recoveries. This corresponds to a fishing mortality of 0·378. Knowing the total catch, and assuming that the calculated F reflects the fishing mortality on the untagged stock, the state of the untagged stock can be estimated using Equation (6).

In principle this method uses the recoveries from the releases which have been at liberty for $2^1/_2$ years or more to determine the state of the tagged stock and exploitation, whereas the recoveries from the releases at liberty for $1^1/_2$ years are used to determine the recruitment to the tagged population. Thus the estimates obtained do not depend on knowing the tagging survivals s. In Table 15 the results of VPA runs on the separate releases are given, starting with a common F of 0·38 in 1977. In the column to the left are shown the corresponding calculated tagging survivals s.

The results of tagging mackerel in the Celtic Sea have shown that the fishery in the North Sea, particularly that in the Shetland area during summer, is based on a mixed stock of North Sea and Western mackerel. In the years prior to 1976 the catch of mackerel from the Western stock in the Shetland area has been estimated from the equation given by Hamre (1978):

$$1 - p_j = \frac{(C_j)_{\mathrm{N}}}{(C_j)_{\mathrm{S}}} \cdot \frac{\left(\sum r_{ij}\right)_{\mathrm{S}}}{\left(\sum r_{ij}\right)_{\mathrm{N}}} \tag{8}$$

where:

- p_j is the proportion of the North Sea stock in the Shetland catches of the year class under consideration in year j;
- $(C_j)_{\mathrm{N}}$ is the catch of that year class taken in the North Sea area in year j which was effectively screened for tag recoveries;
- $(C_j)_{\mathrm{S}}$ is the catch of that year class taken in the Shetland area in year j which was effectively screened for tag recoveries;
- $\Sigma\, r_{ij}$ are the recoveries of fish of that year class in the year in question summed over all releases, with the subscripts S and N denoting recoveries from the Shetland and northeastern North Sea areas respectively.

For 1976 and 1977 it was not possible to split the tag recoveries into the Shetland area (Sh) and the northeastern North Sea (NS), and the Western stock component of the catch in division IVa had to be estimated by a different method. For this purpose it was assumed that all 3-year-old mackerel caught in division IVa were from the North Sea stock.

The proportion of the North Sea stock in the IVa catches of the older age groups was estimated by

$$p_{j+1} = \frac{p_j\ (r_{ij+1} / C_{j+1})}{\Sigma\, r_{ij} / \Sigma\, C_j} \tag{9}$$

Table 16. State of tagged stock and fishing mortality rate. 1969 and older year classes

	Year of recapture														
	1973			1974			1975			1976			1977		
Year of release	*s m*	*r*	*F*	*s m*	*r*	*F*	*s m*	*r*	*F*	*s m*	*r*	*F*	*s m*	*r*	*F*
1969, 1970	848	169	0·230	592	126	0·248	405	78	0·221	285	57	0·231	197	57	0·35
1971	3 650	727	0·230	2 547	–	–	–	–	–	–	–	–	–	–	–
1969, 1970, 1971	–	–	–	3 139	681	0·253	2 139	–	–	–	–	–	–	–	–
1972	–	–	–	4 651	1 009	0·253	3 174	–	–	–	–	–	–	–	–
1969, 1970, 1971, 1972	–	–	–	–	–	–	5 313	1 107	0·242	3 663	–	–	–	–	–
1973	–	–	–	–	–	–	2 731	569	0·242	1 882	–	–	–	–	–
1969, 1970, 1971, 1972, 1973	–	–	–	–	–	–	–	–	–	5 545	1 125	0·235	3 850	–	–
1974	–	–	–	–	–	–	–	–	–	971	197	0·235	674	–	–
1969, 1970, 1971, 1972, 1973, 1974	–	–	–	–	–	–	–	–	–	–	–	–	4 524	1 381	0·378
1975	–	–	–	–	–	–	–	–	–	–	–	–	1 588	485	0·378

where C_j is the catch of the year class in year j effectively screened for tags, Σr_{ij} the recoveries of fish of that year class in year j summed over all releases prior to year j, and p_j the proportion of the IVa catches belonging to the North Sea stock in year j. The estimated proportions are given in Table 17 for the years 1972–1977 (Anon., 1978). It should be noted that Equation (9) is similar to the recruitment Equation (5), and in fact measures the "recruitment" to the North Sea year classes after age 3.

It is reasonable to believe that during the years prior to 1976 the split of r among areas was also incomplete owing to delay in the reporting of tags in relation to the time when they were caught. This may have underestimated the proportion p, using Equation (8), considerably. However, the Celtic Sea releases have shown that even the catches in the eastern North Sea (C_N) may partly consist of Western mackerel. This will overestimate the calculated proportion and thus reduce the effect of the former type of error in the estimates.

The limitation in the use of Equation (9) refers to the difficulties in establishing the fraction r_{ij}/C_j when the year class is only 3 years old. For year classes which are comparatively weak in the Western stock, this age may be extended to 4, which may increase the precision of the estimate considerably. It is noted that an error in this fraction will cause an inverse error in the estimated proportion throughout the life of the year class.

With respect to the tagging in the Celtic Sea, this has so far given data of limited use because returns and corresponding catch are available from the North Sea only, and not from the area of tagging. This makes it uncertain to what extent the tagged population in the North Sea represents the Western stock as a whole. However, assuming random mixing of the tagged fish with respect to each of the separate stocks, the fraction of the catch originating from each of the two stock components can be formulated according to two Petersen stock estimates:

$$C_W = (N_W\, r_W)/(s_W\, m_W)$$

$$C_N = (N_N\, r_N)/(s_N\, m_N)$$

where $C_W + C_N$ = total catch.

The subscripts W and N denote Western and North Sea stocks respectively. Dividing the two formulated catch fractions one gets:

$$\frac{C_W}{C_N} = \frac{s_N\, m_N}{s_W\, m_W} \cdot \frac{N_W}{N_N} \cdot \frac{r_W}{r_N} \tag{10}$$

This equation provides, under the stated condition, an estimate of the catch fraction if the relative sizes of the two stocks are known or vice versa. This method was first used to estimate the contribution of river races of salmon to a common oceanic fishery (Junge and Bayliff, 1955). A similar consideration was made by Hamre (1978) for obtaining a size estimate of the Western stock contributing to the Shetland fishery, and by Walsh (1977) to estimate the contribution of the North Sea and Western stocks to the mackerel fishery in the Minch.

Table 17. Proportion of catch in division IVa attributable to the North Sea mackerel stock (Anon., 1978)

	Year					
Year class	1972	1973	1974	1975	1976	1977
Pre-1969	0·74	0·41	0·58	0·45	0·56	0·75
1969	1·00	0·93	0·71	0·80	0·47	0·71
1970	–	1·00	0·58	0·50	0·65	0·32
1971	–	–	1·00	0·92	0·29	0·51
1972	–	–	–	1·00	0·27	0·55
1973	–	–	–	–	1·00	0·94
1974	–	–	–	–	–	1·00

Results

North Sea stock

The first attempt to assess the North Sea mackerel stock was based on the within-season recoveries of tagged mackerel in the autumn of 1969, assuming a tagging survival coefficient of 0·90. The estimate was an adult stock size, in August 1969, of 850000 t. Although the tagging survival s was considerably overestimated, this has later turned out to be a reasonable estimate. The catch on which it was based was taken in the tagging area soon after release, and the error introduced due to incomplete mixing reduced the estimate in about the same proportion as the error in the s-value increased it.

This estimate of stock in 1969 was used as input in a VPA, back-calculating the stock to 1964 (Fig. 9). In this VPA an M of 0·20 was applied (Hamre, 1970). This may have overestimated the stock in the mid-1960s by about 25%.

Stock size and mortality estimates were obtained during the period 1970 to 1973 using Equations (4) and (3) respectively. By comparing the mortality estimates with the corresponding catch for releases which had been subjected to different levels of fishing mortality it was suggested that the applied natural mortality in the North Sea stock should be reduced to 0·15. The study also indicated that the tagging survival of 90% was too high and a reduction to 0·85 was suggested. Using these revised estimates and the catch, the stock size and fishing mortality were estimated for the years 1965 to 1973. The stock size which refers to August each year and the mortality in the following 12 months are shown in Figure 15 (Hamre, 1978).

Based on this study it was concluded that before the purse-seine fishery was introduced in the mid-1960s, the adult North Sea stock may have fluctuated in size about a level of 2·5 million tonnes. The total catch was below 100000 t, corresponding to a fishing mortality less than 0·04. The stock was thus under-exploited. From 1965 onwards the fishing mortality rose gradually, reaching a peak in 1968–1969 of 0·78. In 1968 and 1969 even the one- and two-year-old fish were heavily exploited, leading to a very rapid decline in the stock in the late 1960s. In 1971, the adult stock was fished down to about 250000 t. By 1972, the stock increased to about 1·5 million tonnes, owing to recruitment from the very strong 1969 year class.

The stock sizes and mortality estimates for the years 1972–1977 given in Table 8a are derived from the catch at age statistics and from the results from tagging (Anon., 1978). Catch in number by ages and years were allocated to the North Sea stock using the proportion of the IVa catches calculated by Equations (8) and (9) and shown in Table 17. A VPA was then run using an M of 0·15 and a terminal F in 1977 of 0·30, which gave the best fit to the mortality estimates in 1974–1976 derived from tagging. The numbers were converted to weight by the weight at age given in Table 3. The stock biomass and fishing mortality of the ages 3 years or older are shown in Figure 15. It can be seen that the calculated stock size and mortality rate in 1972 are in reasonably good agreement with the estimate given by Hamre (1978). Since 1972 the stock has declined continuously even though it has been moderately fished. It is therefore concluded that the stock is now suffering from recruitment failure (Anon., 1978).

The fishing mortality estimates for the years 1974–1977 obtained from tagging (Table 16) are slightly higher than those seen in Table 8a. If the terminal fishing mortality is underestimated, the VPA correspondingly overestimates the stock size. In using tagging data for assessment purposes it is a common experience that the sources of error tend to cause overestimation of the stock size. This has also been the case in the mackerel tagging programme in which the stock size has been revised downward when improved data have become available. Although the analysis presented in Table 16 is preliminary, owing to the lack of completed series of recoveries, and is not to be considered conclusive, it does indicate that the stock estimates shown in Figure 15 still represent a certain overestimate and a corresponding underestimate of the fishing mortality rates.

Western stock

Table 14b gives the calculated survival of the Celtic Sea releases based on between-release estimates (Equation (3) and Robson's method). The 1970 and 1971 estimates seem reasonable, but the estimates for the later years are unrealistic. This may be caused by variation in tagging survival, but it is more likely that the large variation in the calculated survival is caused by non-random mixing of the tagged fish. The catches from which the recoveries are made were all taken far to the north of the area of tagging, and changes in migration pattern from year to year may affect the survival estimates considerably.

Rearranging Equation (10) one can write:

$$(N_W/N_N)_i = \frac{[(s_W/s_N)(m_W/m_N)]_i}{(C_W/C_N)_j\,(r_N/r_W)} \qquad (11)$$

which expresses the relative proportional size $(N_W/N_N)_i$ of the stocks at a given time i as a function of the fraction of surviving tagged fish $(s_W\, m_W/s_N\, m_N)_i$, the catch proportion $(C_W/C_N)_j$ in year j and the fraction of recoveries $(r_N/r_W)_{ij}$ from the release i

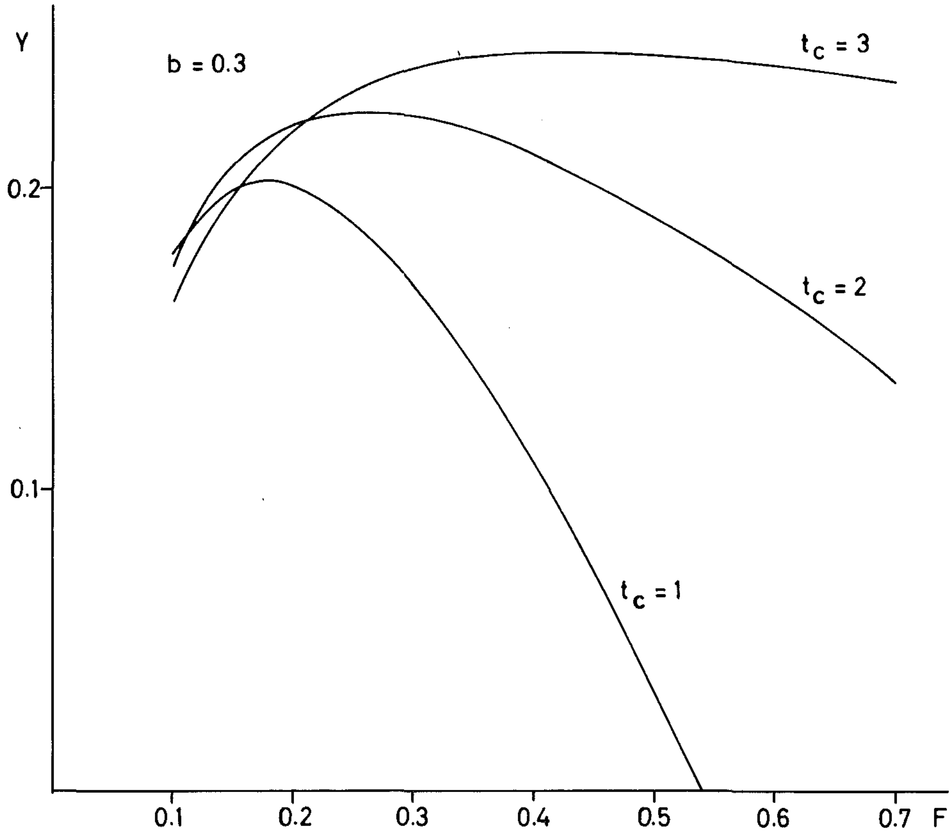

Figure 18. Estimated yield (Y in million tonnes) by fishing mortality (F) and age at first capture (t_c) for density-dependent recruitment (R). $R = N/(aN+b)$ when N equals spawning stock. The asymptotic value $1/a$ is 2000 million individuals (Hamre and Ulltang, 1972).

caught in year j. The $s_W/s_N \approx 0{\cdot}70$ is known from a test experiment carried out in 1971 (Hamre, 1978). The catch $(C_W/C_N)_j$ can be calculated from Table 17 and the fraction $(r_N/r_W)_{ij}$ from Tables 10 and 11. If the conditions for using Equation (10) are satisfied, an index of relative stock size will be available, and N_W when N_N is known. The calculated indices of relative stock size by releases and years are shown in Table 18. The columns on the right in the table show the arithmetic mean and the relative stock-size indices which can be calculated from the data in Tables 8a and 8b.

If the use of Equation (11) is justified the variation of $(N_W/N_N)_{ij}$ by year j should fall within the limits of an acceptable random variation of the estimates. It seems fair to conclude from Table 18 that other sources of variance are reflected in the estimates besides those randomly distributed. It can be seen that since 1975 there has been a systematic decrease in the index of relative abundance for all the releases except the last one, the decrease being most distinct in the releases before 1974. This refers to the year classes older than the 1969 year class. It may also be noted that the computed relative size of the Western stock by this method is considerably smaller than that obtained from Table 8.

Equations (8) and (9) calculate the contribution to the catch from the North Sea stock only; the rest of the catch may not necessarily be mackerel spawning in the Celtic Sea. The fraction r_N/r_W compensates for the contribution from the Celtic Sea spawners only. If there are other stock components involved, the $(N_W/N_N)_{ij}$ will vary by j according to the contribution of the others to the common catch in the year j. Under such conditions, Equation (11) is not valid because the sum C_W+C_N will be less than the total catch. The conditions necessary for an unbiased estimate of this type are in general very extensive (Jung and Bayliff, 1955), and one cannot place much confidence in the results obtained by using the Celtic Sea releases and recoveries for assessment of the Western stock.

Table 18. Relative stock size estimate (N_W/N_N) based on tagging. WG denotes the corresponding index obtained from the ICES Working Group Report 1978. $A_i = \{(s_W m_W)/(s_N m_N)\}_i$. For further explanation see text.

	j:	1972	1973	1974	1975	1976	1977		
	$(C_W/C_N)_j$:	0·35	1·44	0·72	1·22	0·79	0·33	Mean	WG
Pre-1969									
i	A_i								
1971	1·43	1·30	2·43	1·66	4·59	1·93	0·63	2·09	–
1972	1·67	–	3·39	1·66	3·22	2·18	1·40	2·37	5·9
1973	1·83	–	–	3·15	9·78	4·12	2·26	4·83	6·0
1974	3·59	–	–	–	2·01	1·93	1·30	1·75	6·5
1975	4·63	–	–	–	–	1·57	2·20	1·89	6·6
	$(C_W/C_N)_j$:			0·41	0·25	1·13	0·41		
1969									
i	A_i								
1973	0·49	–	–	3·06	1·27	4·63	3·21	3·0	1·55
1974	0·57	–	–	–	0·51	2·34	1·38	1·41	1·76

RECRUITMENT AND SUSTAINABLE YIELD

In the period 1962 to 1971 two strong year classes were observed in the North Sea stock with the 1962 and 1969 year classes respectively recruiting about 3500 and 2000 million individuals as one-year-old fish. The poorest year class observed was the 1970 year class, which recruited some 300 million individuals. The average recruitment from the 1962–1971 year classes was 1290 million individuals. This corresponds to a maximum sustainable yield (MSY) of about 250000 t, provided the fishing mortality is regulated to an F of 0·30, fish less than 30 cm are protected, and the main catch is taken in autumn when the weight at age is at its maximum. The corresponding equilibrium spawning stock level is estimated to be one million tonnes (Hamre, 1978; Hamre and Ulltang, 1972).

None of the year classes recruiting after 1969 has been above 600 million individuals, although the spawning stock has been above the 1969 level for several years (Fig. 15). At present the stock is below the level which, in previous years, has produced year classes of average strength, and a further decline in the spawning stock is expected (Anon., 1978). The future prospects for the North Sea mackerel stock are therefore not very encouraging.

Similar recruitment estimates of the Western stock are available for the 1970s only (Table 8b). During this period the recruitment has remained high, ranging from 1454 million to 7380 million individuals for the 1972 and 1975 year classes respectively. Assuming that before 1975 the equilibrium state of the Western stock, including all the year classes of one year or older, has been about $17–18 \times 10^9$ individuals (Table 8b) this corresponds to an average annual recruitment at age one of about 3500 million individuals for the appropriate level of total mortality rate (about 20%).

FISHERIES REGULATIONS

Apart from a NEAFC recommendation which prohibited fishing in the North Sea for mackerel smaller than 30 cm for reduction purposes, no effective international fishery regulation has been applied in the Northeast Atlantic mackerel fisheries. Since 1970, the Norwegian mackerel fishery for reduction purposes has been subject to national regulations. This fishery accounted for more than 80% of the North Sea catches in the late 1960s and the national regulations imposed on this fishery have therefore been of major importance for the conservation of the North Sea mackerel stock.

The regulations of the Norwegian industrial fishery include: minimum landing size of 30 cm, closed season and areas, and catch quota regulation. The effects of these regulations on stock and yield were studied by Hamre and Ulltang (1972), and the following conclusions were drawn:

1) The gain in yield obtained by a minimum legal size is rather small. The regulation affects, however, the size of the spawning stock considerably. The spawning stock biomass may be increased by 100% by increasing age at first capture from 1 to 3 years (22 cm–32 cm) when the fishing mortality is above 0·4 (Figs. 16 and 17).
2) The closed season regulation has a considerable effect on both the yield and the spawning stock, especially when the fishing mortality is high and the younger age groups are unprotected. Fishing during summer and autumn is most favourable and may increase the yield and spawning stock by about 20% compared with an equal distribution of effort throughout the year. The winter fishery represents the most unfavourable fishing strategy. The Norwegian industrial fishery has been pro-

hibited from November to July and the seasonal distribution of effort resulting from this was found to be close to that giving optimum values of stock and yield.

3) The state of stock and yield was also considered by assuming density-dependent recruitment (Fig. 18). It was found that if the recruitment is density-dependent the risk of overexploitation occurs when the fishing mortality exceeds 0·3. Since the expected gain in sustained yield by increasing fishing mortality above 0·3 was in any case found to be rather small, an F of 0·3 was suggested as a guideline for the determination of the total allowable catch (TAC).

The fishing mortality rate of the North Sea stock in the 1970s has been well below this recommended level, resulting in an increase in spawning stock size to about 1·5 million t in 1972. Since 1973 the stock has declined on account of poor recruitment, but the rate of decline has no doubt been considerably reduced by the regulation of the Norwegian mackerel fishery.

The North Sea area south of 60°N has been closed to Norwegian purse seiners until the middle of September, whereas the area north of 60°N has been opened in July. This area regulation is applied in order to divert fishing effort from the central area of distribution of the North Sea stock to an area where the stock is mixed with other stock components which may still be underexploited. This regulation was not put into force in 1977, which explains the relatively high proportion of catch attributed to the North Sea stock in 1977 (Table 17, year classes 1969 and older).

The ICES Mackerel Working Group was concerned about the low recruitment to the North Sea stock in the 1970s (Anon., 1975). In order to maintain an adequate spawning stock the Working Group recommended, in the current stock situation, applying a TAC calculated at an F of 0·20. This F was selected by considering the effects of a possible stock-recruitment relationship similar to that used for computing the yield curves in Figure 18. The TAC advice for later years is all calculated on that basis of fishing mortality.

CONCLUDING REMARKS

The Northeast Atlantic mackerel are mainly distributed in the continental shelf area between 43°N and 62°N (ICES statistical sub-areas III–VIII). In a virgin state, the stock biomass may have fluctuated at a level of 10 million tonnes. After herring, mackerel are thus the most important exploited plankton feeder in this area.

Two main spawning areas of mackerel are distinguished, the North Sea and the Celtic Sea. The mackerel is however a highly migratory fish and its range of migration during the feeding period covers its main areas of distribution. Although separate spawning races may exist, the state of the stock as a whole is of importance for the fisheries on both sides of the British Isles.

Before the 1960s, mackerel were underexploited, owing to limited market demand and low gear efficiency for catching this fast-swimming fish. This situation was changed in the mid-1960s by the introduction of the large-scale industrial fishery in the North Sea aimed at herring and mackerel. The North Sea mackerel stock became heavily overfished and the adult stock was at the point of being fished out completely by the end of the 1960s.

The state of exploitation of mackerel remained more or less unchanged in the area west of the British Isles. This resulted in a drastic change in the balance between the North Sea and the Western mackerel stock with respect to the size of the populations. From the early 1970s onwards, extensive annual migrations have taken place from the spawning ground in the Celtic Sea to the mackerel feeding areas of the North Sea. This may be related to the very large change in the relative abundance in the two areas.

This migratory pattern has been of vital importance to the North Sea mackerel fishery in the 1970s. Apart from contributing a major share of the catch, which was in fact necessary for the North Sea fishery to remain profitable, the influx of Western mackerel changed the time and main area of fishing compared with previous years. This had an impact on the seasonal fishing activity of the fleet, which again affected the allocation of effort to other fisheries. The occurrence of a fishery based on a mixed stock raised, moreover, new and important questions, with respect to the assessment of the separate stocks involved and to the management of the fishery.

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