

INTERNATIONAL COMMISSION
FOR THE
NORTHWEST ATLANTIC FISHERIES



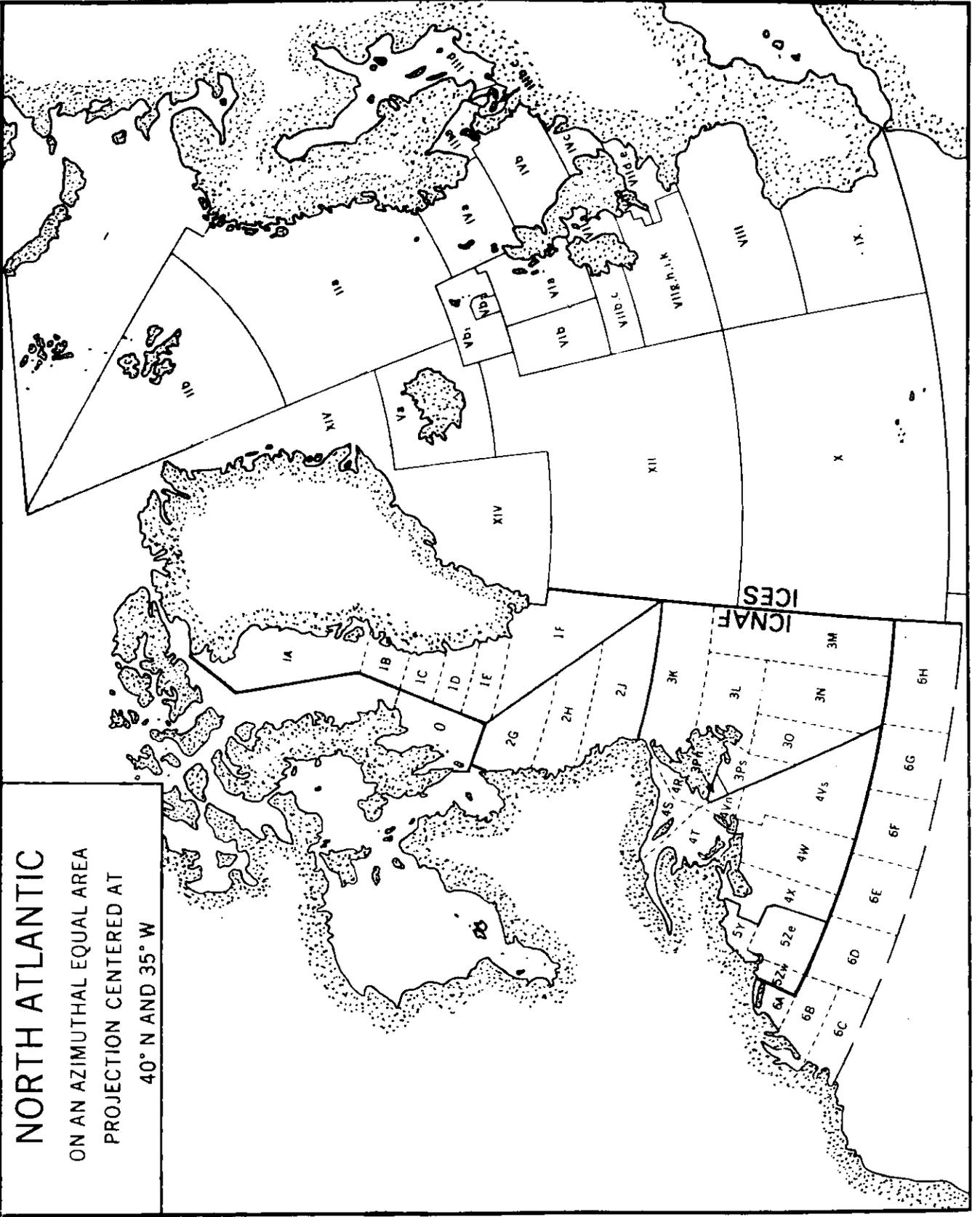
Selected Papers
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Foreword

This issue of Selected Papers is the first in the new series to be published annually or more frequently, depending on the number of contributions. During the period 1958 to 1973, selected papers from ICNAF Meetings were published in the Redbook series.

Papers for publication in this new series are selected, subject to the approval of the authors, by the Steering and Publications Subcommittee of STACRES (Standing Committee on Research and Statistics) from papers presented to scientific meetings of ICNAF. In general, the papers selected contain information which is considered worthy of wider circulation than is normal for meeting documents. Each author is supplied with 50 reprints of his or her contribution.



NORTH ATLANTIC
 ON AN AZIMUTHAL EQUAL AREA
 PROJECTION CENTERED AT
 40° N AND 35° W

ICNAF

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Eastern Scotian Shelf Cod: A Reconstruction of Possible Events in the Fishery in 1958 to 1974 and a Re-estimation of Potential Yield¹

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ABSTRACT

Cod catches in ICNAF Subdivision 4Vs and Division 4W averaged 60,000 metric tons over the 15-year period, 1960-74, but have been lower than this average in most recent years. Commercial catch rates suggest that a decline occurred in the early 1970's in the cod stocks supporting these catches to levels substantially below those prevailing in the 1960's. Recent improvements in biological sampling of commercial catches confirm that substantially greater proportions of small fish are removed by the fishery than suggested by previous analyses. Re-analyses of stock status, using one possible set of assumptions on the historical size composition of removals based on these new data, suggest that the stocks have been subject to reduced recruitment and gross over-fishing in most recent years, and a reduction in catch to 30,000 tons or less in 1976 is required to initiate recovery towards the stock level giving maximum sustainable yield.

INTRODUCTION

Assessment of the status of the cod stock complex in ICNAF Subdiv. 4Vs and Div. 4W has been hindered by the low level of biological sampling of commercial catches. Increased sampling efforts by Spain and USSR in the 1970's established that the catches of these countries are substantially different in size and age composition from those of Canada. An earlier yield assessment of these stocks (Halliday, 1972) was based on the assumption that Canadian sampling data were representative of all removals from the stocks. Inconsistencies in the results of that analysis imply that the differences in size and age compositions seen in the sampling data for the early 1970's were important also in the 1960's.

In the present analysis, country, division and seasonal stratifications are used in applying sampling data to catches in estimation of removals from the stocks. Available sampling data are inadequate to meet the demands of this detailed stratification and a variety of assumptions are required. The primary assumptions are that the size compositions of Spanish and USSR catches in the 1960's were similar to those in the 1970's.

GROWTH

Halliday (1972) fitted a von Bertalanffy growth curve to average mean lengths of ages 6-10 cod in 1960-71 Canadian commercial samples from Subdiv. 4Vs and Div. 4W combined. New data, particularly from research vessel surveys, allow refinement of growth estimates.

Mean length at age from Canadian commercial sampling data were calculated for each of three 5-year periods for January to June and July to December samples from Subdiv. 4Vs and Div. 4W separately (Table 1). Mean lengths at age are also available from Canadian research vessel surveys conducted in July of 1970-74 in Subdiv. 4Vs and Div. 4W (Table 2).

¹ Submitted to the Seventh Special Commission Meeting, September 1975 as Res.Doc. 75/IX/136.

Table 1. Cod in Subdiv. 4Vs and Div. 4W: Mean length at age in Canadian commercial samples. (Parentheses indicate that representation in the catch is less than 1%.)

Area	Period	Mean length (cm) at age								
		3	4	5	6	7	8	9	10	
4Vs	Jan-Jun	1960-64	(46.0)	47.0	53.3	56.7	63.6	62.3	63.2	(74.7)
		1965-69	37.5	45.7	52.1	55.9	61.1	60.2	63.4	66.1
		1970-74	(42.2)	44.2	50.7	55.9	61.5	65.0	72.6	75.9
		Average	(41.9)	45.6	52.0	56.2	62.1	62.5	66.4	(72.2)
4Vs	Jul-Dec	1960-64	40.6	48.3	52.6	63.4	72.7	71.3	81.3	(94.0)
		1965-69	39.3	46.9	52.1	57.3	67.0	(73.4)	(85.0)	-
		1970-74	43.8	47.4	53.9	62.1	63.1	75.6	82.2	88.9
		Average	41.2	47.5	52.9	60.9	67.6	73.4	(82.8)	(91.5)
4W	Jan-Jun	1960-64	(47.1)	49.8	55.7	60.6	65.1	69.0	76.2	87.7
		1965-69	42.8	48.9	54.7	60.4	67.0	74.2	79.8	86.5
		1970-74	39.0	45.6	51.6	57.5	63.4	64.8	67.7	77.4
		Average	(43.0)	48.1	54.0	59.5	65.2	69.3	74.6	83.9
4W	Jul-Dec	1960-64	46.4	49.5	54.6	62.9	69.5	74.6	(87.3)	(81.4)
		1965-69	45.0	50.6	56.9	64.1	75.9	(82.5)	(86.0)	(73.2)
		1970-74	45.8	51.3	57.2	59.4	63.8	64.0	(92.8)	(77.6)
		Average	45.7	50.5	56.2	62.1	69.7	(73.7)	(88.7)	(71.4)

Table 2. Cod in Subdiv. 4Vs and Div. 4W: Mean length at age in research vessel survey sampling data. (Parentheses indicate that representation in the catch is less than 1%.)

Area	Year	Mean length (cm) at age								
		1	2	3	4	5	6	7	8	9
4Vs	1970	(16.8)	26.2	40.3	48.3	53.5	58.6	64.3	(65.0)	-
	1971	-	28.6	36.3	44.1	52.1	57.0	56.6	62.9	(70.0)
	1972	(22.9)	31.8	41.9	44.8	53.0	57.1	57.0	(63.3)	(91.0)
	1973	21.6	31.5	41.2	47.9	55.9	-	-	-	-
	1974	21.1	31.1	38.4	47.0	53.1	58.8	(62.6)	67.5	67.0
	Average	21.4	29.8	39.6	46.4	53.5	57.9	59.3	65.2	-
4W	1970	20.6	35.7	45.7	51.7	59.3	69.4	77.8	(77.0)	(79.0)
	1971	16.7	24.6	38.7	51.2	56.1	59.9	67.1	67.8	74.9
	1972	19.7	31.3	43.2	55.0	59.7	65.9	(82.0)	(79.0)	(98.0)
	1973	21.6	29.5	38.9	48.0	52.1	(61.1)	(60.2)	(88.0)	-
	1974	20.3	32.2	38.6	47.5	54.5	(62.5)	(70.5)	(61.9)	(62.6)
	Average	19.8	30.7	41.0	50.7	56.3	65.1	72.5	67.8	74.9

There are no consistent trends in length at age with time. Decreases in the size of 4- and 5-year olds between 1960-64 and 1970-74 in January-June in both Subdiv. 4Vs and Div. 4W and increases in the size of these age-groups in July-December in Div. 4W may reflect trends in the average time of sampling within the 6-month periods. Thus, the mean lengths in commercial samples between 1960 and 1974 and in surveys from 1970 to 1974 were used in constructing growth curves. Commercial January-June data were taken as an estimate of length of, say, 3-year olds at age 3.25, survey data at age 3.50, and commercial July-December data at age 3.75. There is close agreement between commercial and survey lengths at age (Fig. 1). Div. 4W cod are slightly larger than Subdiv. 4Vs cod of the same age after age 1.

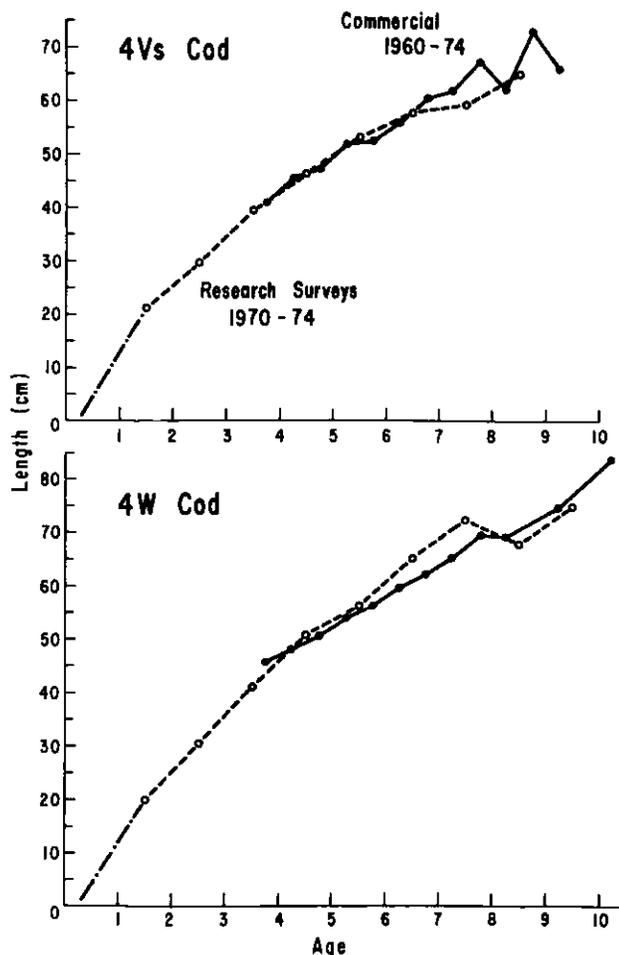


Fig. 1. Div. 4VsW cod. Mean length at age of Div. 4Vs and Div. 4W cod from Canadian research vessel surveys and Canadian commercial samples.

Von Bertalanffy growth curves were fitted to data for ages 1.5 to 9.25 for Subdiv. 4Vs cod and for ages 1.5 to 10.25 for Div. 4W cod giving the following parameters:

Parameter	Subdiv. 4Vs	Div. 4W
K	0.15	0.14
t_0	-0.21	-0.07
L_∞	89.9 cm	102.5 cm
(W_∞)	(7.12 kg)	(10.37 kg)

YIELD PER RECRUIT

Beverton and Holt yield-per-recruit isopleth diagrams were constructed to examine the effects of differences in growth parameters between Subdiv. 4Vs and Div. 4W (Fig. 2). No estimate of natural mortality (M) is available for these stocks; but a value of $M = 0.20$, which appears to be generally applicable to Northwest Atlantic cod stocks, was assumed. Other parameters used in the calculations are:

- t_p - 1.0 yr (age at recruitment to the fishing area),
- t_p^1 - varied between 1.0 and 6.0 yrs (age at recruitment to the exploited phase), and
- t_λ - 25 yrs (maximum age of significant contribution to the fishery).

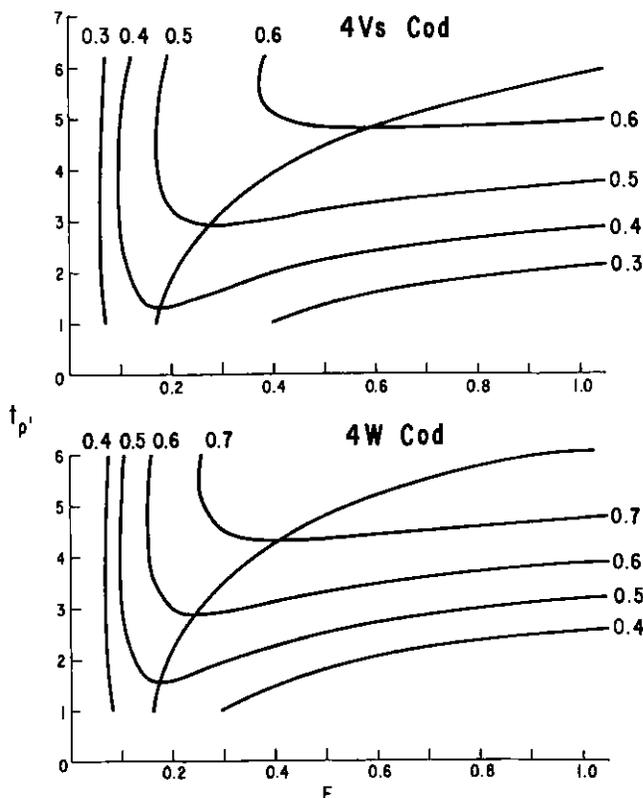


Fig. 2. Div. 4VsW cod. Yield per recruit isopleth diagrams for Div. 4Vs and Div. 4W cod. F = instantaneous fishing mortality, t_p^1 = age at recruitment to the exploited stock, numbers in body of graph are yields per recruit in kg.

Yield per recruit from Div. 4W cod is higher than that from Subdiv. 4Vs cod for the same age at recruitment to the fishery and fishing mortality rate (F). Over the range of t_p^1 and F likely to prevail in the fishery the difference is approximately 20%.

The yield isopleth diagram presented by Halliday (1972) for Subdiv. 4Vs and Div. 4W combined gives intermediate values to those for Subdiv. 4Vs and Div. 4W presented here, but is most similar to that for Div. 4W and thus, probably overestimates the yield per recruit from the eastern Scotian Shelf cod as a whole.

NOMINAL CATCHES

Cod catches from Subdiv. 4Vs and Div. 4W have averaged 60,000 tons over the 15-year period 1960-74 (Table 3), but have been lower in most recent years (1970-74 average = 54,000 tons), 1974 catches being only 43,700 tons. Catches have been fairly equally distributed between divisions. Spain has been the major exploiter of these stocks taking 61% of the yield over the last 15 years, followed by Canada taking 28%. Catches by the USSR have not exceeded 10,000 tons in any year and, except in 1963-66, have been less than 5,000 tons. Catches by France and Portugal were significant in the late 1950's, and moderately large catches by Denmark have occurred in the early 1970's. Catches in Table 3 for 1958 particularly, but also up to 1962, are subject to error, as not all countries reported their catches from Subdiv. 4Vn and 4Vs separately until 1963. The catch breakdown given by Hodder (MS 1972) is used here.

Table 3. Cod in Subdiv. 4Vs and Div. 4W: Nominal catches (metric tons) by country and division, 1958-74.

Year	Canada	France	Portugal	Spain	USSR	Others	Total	Subdiv. 4Vs	Div. 4W	TAC
1958 ¹	17,938	4,577	1,095	14,857	-	124	38,591	23,790	14,801	-
1959 ¹	20,069	16,378	8,384	19,999	-	1,196	66,026	47,063	18,963	-
1960 ¹	18,390	1,018	1,720	29,391	-	126	50,645	27,689	22,956	-
1961 ¹	19,697	3,252	2,321	40,884	113	42	66,309	34,237	32,072	-
1962 ¹	17,579	2,645	341	42,146	2,383	60	65,154	26,350	38,804	-
1963	13,144	72	617	44,528	9,505	307	68,173	27,566	40,607	-
1964	14,330	1,010	-	39,690	7,133	1,094	63,257	25,496	37,761	-
1965	23,104	536	88	39,280	7,856	124	70,988	36,713	34,275	-
1966	17,690	1,494	-	43,157	5,473	356	68,170	27,163	41,007	-
1967	18,464	77	102	33,934	1,068	512	54,157	26,607	27,550	-
1968	24,888	225	-	50,418	4,865	29	80,425	48,781	31,644	-
1969	14,188	217	-	32,305	2,783	664	50,157	22,309	27,848	-
1970	11,818	420	296	41,926	2,521	446	57,427	28,632	28,795	-
1971	17,064	4	18	30,864	4,506	107	52,563	24,128	28,435	-
1972	19,987	495	856	28,542	4,646	7,119	61,645	36,533	25,112	-
1973	15,929	922	849	30,883	2,918	2,569	54,070	23,401	30,669	60,500
1974 ²	10,701	29	1,464	27,380	3,097	1,075	43,746	19,597	24,149	60,000

¹ Nominal catches reported as Div. 4V and assigned as given by Hodder (MS 1972).

² Preliminary catch statistics.

CATCH PER UNIT EFFORT

Halliday (1972) reviewed available catch per effort data for cod in Subdiv. 4Vs and Div. 4W and chose the catch rates of Spanish pair trawlers of 151-500 gross tons during their peak fishing period of February to April inclusive as the most useful indicator of cod abundance.

Catch rates of these vessels in Subdiv. 4Vs increased from 1.37 t/df (metric tons per day fished) in 1960 to a peak of 2.08 t/df in 1965, declined in 1966 but increased to a peak of 2.36 t/df, in 1968. Subsequently, catch rates steadily declined to 0.74 t/df in 1973, the lowest catch rate in the 14 year data series (Table 4). In Div. 4W, catch rates fluctuated between 1.15 and 1.59 t/df in 1960-67, then peaked sharply in 1968 at 2.39 t/df. Catch rates then declined steadily to a low of 0.68 t/df in 1972, with a slight increase to 0.87 t/df in 1973.

Table 4. Cod in Subdiv. 4Vs and Div. 4W: Catch rates (tons per hour fished) of Spanish pair trawlers (151-500 GRT) in the February to April period, 1960-73.

Area	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
4Vs	1.37	1.53	1.45	1.72	1.77	2.08	1.70	1.83	2.36	1.60	1.61	1.18	1.12	0.74
4W	1.22	1.51	1.24	1.40	1.32	1.15	1.59	1.51	2.39	1.80	1.45	1.32	0.68	0.87

Interpreting these data in terms of cod abundance, it is apparent that there has been a serious decline in the cod stocks of both divisions in the early 1970's to levels substantially below those prevailing in the 1960's. Catch rates were slightly higher in Subdiv. 4Vs than in Div. 4W from 1960 to 1967, although the Div. 4W catch rate was the higher in four of the subsequent six years. There are similarities in overall trends, particularly in the exceptionally high catch rates in both areas in 1968 and in the sharp declines in the following years.

ESTIMATED REMOVALS FROM THE STOCKS

Methodology

Review of Canadian commercial sample age compositions by 5-year periods, division, and season (Table 5) revealed substantial differences in age composition between divisions

Table 5. Cod in Subdiv. 4Vs and Div. 4W: Percentage age compositions in Canadian commercial samples, 1960-74.

Area	Period	Mean age (yr)	Percentage age composition											
			2	3	4	5	6	7	8	9	10	11	12+	
4Vs	Jan-Jun	1960-64	5.7	-	0.9	25.6	23.5	22.8	11.0	11.7	2.9	0.8	0.4	0.5
		1965-69	5.7	0.1	4.0	23.5	30.1	17.8	9.2	6.6	3.9	2.8	1.3	0.8
		1970-74	6.3	-	0.5	12.4	27.6	24.1	13.9	12.9	3.8	2.2	1.1	1.8
4Vs	Jul-Dec	1960-64	4.8	1.1	12.0	32.9	39.1	4.7	2.2	5.9	1.3	0.3	0.3	0.3
		1965-69	5.0	-	1.8	25.2	52.4	17.9	1.7	0.7	0.3	-	-	-
		1970-74	5.7	-	12.5	13.6	29.5	15.6	14.2	7.0	3.0	2.8	0.6	1.1
4W	Jan-Jun	1960-64	6.4	-	0.4	7.5	25.7	25.0	18.7	13.5	5.6	1.4	1.0	1.1
		1965-69	5.9	-	2.5	18.6	27.2	26.5	10.8	6.2	3.9	1.9	1.3	1.3
		1970-74	5.8	-	2.1	18.6	34.7	15.4	11.9	9.6	4.6	1.3	1.6	0.3
4W	Jul-Dec	1960-64	4.7	-	13.7	37.8	26.8	12.5	5.9	2.3	0.4	0.4	0.1	0.1
		1965-69	4.5	0.2	16.1	42.8	26.5	9.9	2.3	1.0	0.5	0.7	0.1	0.1
		1970-74	3.8	10.6	35.2	33.0	10.8	6.0	2.8	1.4	+	0.2	-	+

and seasons and trends with time, catches in Subdiv. 4Vs having a progressively older mean age from 1960-64 to 1970-74, while those from Div. 4W became progressively younger. Examination of Spanish commercial length frequencies for October, 1964, from Subdiv. 4Vs and Div. 4W in the ICNAF Sampling Yearbook indicates that smaller fish were caught by Spain in this season than in February to April for which Spanish samples are available for 1960-62 and 1964. Soviet samples are available for their commercial catches in 1973 and 1974, indicating that the Soviet fleet takes much smaller and younger cod than either Canadian or Spanish fleets.

Thus, country, division, and seasonal stratification of the catches are of major importance in weighting by samples to obtain age compositions of removals. Sampling data are inadequate to sustain this degree of stratification. It is, therefore, necessary to make a number of assumptions on the age composition of catches for which sampling is not available.

USSR sampling data for 1973 and 1974 are consistent in indicating that their catch is largely composed of age 2 and age 3 cod. Labelled as commercial catch samples, the catches were taken with 40 mm mesh nets presumably as a by-catch in the silver hake fishery. The larger cod catches by the USSR in the early 1960's are also entered in ICNAF Statistical Bulletins as by-catches to silver hake effort. It is assumed, then that all USSR catches of cod have had a similar age composition to those of 1973-74, and that catches in 1961-72 were attributed to age-groups on the basis of the average 1973-74 age composition.

Spanish sampling data are available for some months in 1960, 1961, 1962, and 1964. In summary, there are, for Div. 4W, nine samples in the January to June season and nine in the July to December season. For Subdiv. 4Vs, there are seven samples in January-June and two in July-December. These samples, combined as described above, were applied to Spanish catch data for 1958 to 1967 (except for 1962 for which sufficient data were available not to require the use of samples from other years).

Spanish samples are also available for 1971, 1973, and 1974. These are all from the January to June period, and, of 16 samples, only one is from Div. 4W. These samples were applied to Spanish catches in January-June of the respective years in which they were collected. For 1972, the average of 1971 and 1973 samples was applied to catches. For 1968-70, the January-June catches were weighted by all 16 of the 1971-74 samples combined. In 1968-74, no samples were available for the July to December period, and Spanish catches were weighted by Canadian samples from the appropriate season and year.

Canadian sampling data is also sparse but distributed fairly evenly among years, divisions and seasons. Canadian Subdiv. 4Vs catches are almost entirely taken by otter trawl, but insufficient sampling data are available to weight the catches by season. Thus, all Subdiv. 4Vs catches in a particular year were weighted by all the samples for Subdiv. 4Vs in that year (except 1958, 1959, and 1971 when seasonal weighting was possible). Available samples ranged from one to ten. In two years (1961 and 1969), when no samples were available, the averages of adjacent years were used.

Canadian catches in Div. 4W were predominantly by otter trawl between 1960 and 1968 but other gears, primarily inshore, caught approximately 5,000 tons of cod annually during this period. Since 1968, gears other than otter trawls have taken the larger share of the catch and by 1974 only 22% of the Canadian Div. 4W catch was taken by otter trawlers (Table 6).

Table 6. Cod in Subdiv. 4Vs and Div. 4W: Canadian nominal catches (tons) by otter trawl and by other gears, 1958-74.

Year	Subdiv. 4Vs		Div. 4W	
	Trawls	Other gear	Trawls	Other gear
1958	4258	2092	4892	5731
1959	4181	1286	7294	7308
1960	1924	750	10228	5488
1961	1135	136	12895	5531
1962	1495	93	11762	4229
1963	1258	34	7779	4063
1964	2059	41	7324	4906
1965	7366	106	10293	5338
1966	6375	156	6614	4545
1967	6729	132	6463	5140
1968	9501	66	8367	6954
1969	3539	51	4424	6174
1970	3054	22	3596	5146
1971	5826	41	4745	6452
1972	9856	119	4732	5280
1973	6397	77	4723	4731
1974	4640	60	1343	4658

Almost all available sampling data are from otter trawl catches and it has been necessary to assume that catches of other gears had similar age compositions (in all years except 1974, when longline and handline samples were available). The degree of error introduced by this assumption can be judged from the comparisons in Table 7.

Table 7. Cod in Subdiv. 4Vs and Div. 4W: Percentage age compositions of cod caught by otter trawl, longline and handline in Canadian catches from Div. 4W in 1959, 1964, 1968-69, and 1974.

Year	Season	Gear ¹	Percentage age composition											Mean age	Mean length
			2	3	4	5	6	7	8	9	10	11	12+		
1959	Jan-Jun	HL	-	0.4	8.4	13.3	16.5	16.5	13.4	7.7	12.3	6.2	5.3	7.5	71.6
1959		OT	-	0.6	6.1	11.9	10.8	33.2	9.4	6.1	16.7	2.8	2.4	7.4	67.2
1964	Jan-Jun	LL	-	-	-	18.9	11.9	23.1	20.2	20.2	3.2	1.7	0.8	7.3	54.5
1964		OT	-	-	0.8	17.9	14.9	18.4	17.7	17.0	6.8	3.2	3.3	7.5	71.5
1968	Jul-Dec	LL	-	1.0	17.8	21.0	40.3	9.7	6.8	2.5	0.5	0.4	-	5.8	56.6
1968		OT	1.8	32.2	31.8	22.9	8.3	1.8	0.8	-	0.2	-	0.2	4.2	53.0
1969	Jul-Dec	LL	-	0.4	14.5	28.8	24.4	17.2	6.6	1.3	0.8	1.7	4.3	6.2	58.0
1969		OT	-	19.1	40.0	28.6	8.0	1.4	1.7	1.2	-	-	-	4.6	51.5
1974	Jul-Dec	LL ²	2.0	25.0	31.3	20.6	7.3	4.2	5.6	2.4	1.1	0.4	0.1	4.6	55.1
1974		OT	1.6	45.7	38.2	11.3	1.6	0.5	1.1	-	-	-	-	3.7	49.9

¹ HL = handline, OT = otter trawl, and LL = longline

² Includes handline sample.

A seasonal breakdown was possible for Canadian Div. 4W catches, sampling gaps in the July-December period in 1961, 1964 and 1970 being filled by averaging samples from adjacent years for the same season.

The small catches of other countries are assumed to have had the same age composition as those of Canada. USSR samples consist of length frequencies only. The season of capture was similar to that of Canadian research vessel survey operations. Thus Canadian survey age-length keys for the appropriate years were used to obtain age compositions for USSR catches.

Spanish samples include age data but discrepancies between Spanish and Canadian ageing for cod in this area are substantial (Lopez-Veiga *et al.*, MS 1975). For consistency, Canadian ageing data were used throughout, the appropriate Canadian age-length key for a particular division, year and season being applied to Spanish length frequency data.

Results of Analysis

Assuming that USSR catches have been consistently of ages 2 and 3 fish, removals by the USSR were about 23 million fish in 1963, declining in the late 1960's but increasing to about 11 million in 1971 and 1972, and then declining to about 6.8 million in 1974.

Removals by Spain increased from 7.6 million fish in 1958 to 25.7 million by 1963, fluctuating around this level until 1968 when they increased to 38.8 million. Removals have since declined to a low of 19.3 million by 1974.

Canadian removals fluctuated between 8 million and 10 million fish in 1958-64, increasing to 15 million in 1965. Subsequently, they varied between 6.8 million and 13.6 million fish, the lowest number being removed in 1974.

Total removals increased from 19.5 million in 1958 to 57.1 million in 1963, declining until 1968 when removals peaked at 64.2 million. They remained over 40 million until 1974 when 34.5 million fish were removed (Table 8).

Table 8. Cod in Subdiv. 4Vs and Div. 4W: estimated age composition of catches, 1958-74.

Age	Cod removals (thousands of fish)																
	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
1	-	-	-	22	459	1832	1375	1514	1055	206	938	536	486	869	896	533	557
2	138	-	-	139	2928	11681	8874	9667	6726	2057	6120	3420	3488	6025	8261	4763	3298
3	2854	2499	7016	3350	4063	9120	8855	12250	10269	4858	10990	4010	5558	6634	8095	11111	8614
4	3534	8887	6118	9571	9978	10844	7862	11321	12660	7733	16616	13055	14196	8065	12245	6792	9217
5	2533	8811	6655	9334	6253	10441	11423	4953	10139	9370	15245	10026	13472	8449	9289	9441	7024
6	3726	6490	4525	6676	7887	5423	4696	6130	4461	4338	8297	6073	4539	10262	8780	3818	2718
7	1610	4384	2811	2885	2744	4875	2874	3135	3256	1467	3482	2144	1942	5160	3432	2979	944
8	1465	1467	1827	1882	2538	2183	2345	4477	1590	1239	895	510	759	1849	1919	3717	1320
9	2014	878	290	1212	686	346	1047	2127	856	664	816	237	236	496	358	1164	413
10	859	1101	133	169	478	134	312	1583	496	647	361	50	72	114	393	273	369
11	543	318	122	147	169	121	145	172	666	325	152	95	137	131	79	299	15
12	58	251	75	88	75	50	75	91	24	65	211	58	56	72	2	3	5
13	51	27	1	66	68	26	50	96	14	16	33	12	9	98	37	7	-
14	11	-	15	3	-	-	-	88	-	5	17	7	12	12	-	5	-
15	10	-	-	-	5	-	-	163	2	7	1	2	4	51	1	5	-
16+	53	21	6	-	-	1	11	7	1	2	10	2	3	17	1	20	-
Total	19459	35134	29594	35544	38331	57077	49944	57774	52215	32999	64184	40237	44969	48304	53788	44930	34494

RESEARCH VESSEL SURVEYS

Canada has conducted stratified-random groundfish surveys in Subdiv. 4Vs and Div. 4W since 1970. Estimates of population numbers at age from these surveys are very variable (Table 9). Relative year-class strengths appear more stable than absolute abundance estimates, the 1966 and 1968 year-classes consistently showing up as being stronger than those adjacent to them. It is possible that either the 1971 or 1972 year-class is stronger than adjacent year-classes.

It appears from Table 8 that cod of age 6, and, in most recent years, age 5 are fully recruited to the fishery. Estimates of F from survey data for fully recruited age-groups are very variable. The average F for the period 1970-74 is estimated to be about F = 0.60 (Table 9).

Table 9. Cod in Subdiv. 4Vs and Div. 4W: survey population estimates and mortality of fully recruited age-groups.

Age	1970	1971	1972	1973	1974
1	1,480	1,539	6,210	16,128	6,084
2	16,388	7,680	9,657	122,779	32,961
3	5,250	35,664	9,635	104,965	19,246
4	7,669	8,027	33,848	59,948	5,623
5	3,735	15,803	5,571	22,524	2,017
6	1,217	5,771	6,111	1,870	2,244
7	1,502	3,459	1,688	2,907	372
8	462	1,475	547	901	563
9	104	638	495	431	224
10+	711	471	153	910	340
Totals	38,518	80,531	73,915	333,363	69,574
F (age 5+)	-0.62	0.92	0.53	1.67	0.63 ¹
F (age 6+)	-0.61	1.21	0.37	1.41	0.60 ¹

¹ Mean F

FISHING MORTALITY FROM COHORT ANALYSIS

Using the data from Table 8, several trial runs of cohort analysis were performed using different assumptions for F in 1974. It became apparent that F in 1972 and 1973 was high. Thus, a value of F = 0.60 was chosen for fully recruited age-groups in 1974, being the value obtained from research vessel surveys and a likely conservative estimate of 1974 mortality. The selection pattern at age in 1974 was taken as the average selection pattern in 1972 and 1973, the values used being:

Age	Percent Selection
1	1
2	12
3	30
4	51
5+	100

Table 10. Cod in Subdiv. 4Vs and Div. 4W: estimated fishing mortality.

Age	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
1	-	-	-	-	-	0.02	0.01	0.01	0.01	-	0.01	0.01	0.01	0.01	0.01	(0.01)	(0.01)
2	-	-	-	-	0.06	0.16	0.10	0.11	0.07	0.02	0.07	0.07	0.06	0.12	0.12	0.07	(0.05)
3	0.05	0.04	0.12	0.06	0.07	0.25	0.17	0.20	0.17	0.07	0.14	0.06	0.15	0.15	0.23	0.24	0.18
4	0.11	0.20	0.12	0.23	0.26	0.27	0.35	0.34	0.32	0.19	0.36	0.24	0.34	0.33	0.47	0.31	0.31
5	0.13	0.42	0.23	0.28	0.24	0.48	0.50	0.39	0.59	0.42	0.69	0.38	0.41	0.35	0.79	0.83	0.60
6	0.26	0.56	0.40	0.38	0.40	0.33	0.41	0.56	0.73	0.55	0.83	0.66	0.30	0.64	0.74	0.92	0.60
7	0.40	0.57	0.51	0.48	0.27	0.46	0.29	0.54	0.66	0.57	1.26	0.53	0.46	0.66	0.46	0.61	0.60
8	0.60	0.80	0.49	0.79	1.08	0.36	0.42	1.04	0.59	0.57	0.85	0.61	0.36	1.11	0.55	1.47	0.60
9	0.73	0.91	0.35	0.72	0.78	0.39	0.29	0.88	0.56	0.53	0.97	0.57	0.64	0.42	0.66	0.77	0.60
10	0.85	1.27	0.32	0.36	0.70	0.33	0.75	0.96	0.51	1.17	0.63	0.13	0.34	0.74	0.71	2.05	0.60
11	1.02	0.92	0.43	0.72	0.75	0.38	0.72	1.38	1.76	0.77	1.01	0.33	0.63	2.27	2.74	3.15	0.60
Weighted mean 4+	0.23	0.38	0.29	0.32	0.32	0.36	0.40	0.50	0.48	0.34	0.57	0.34	0.37	0.47	0.60	0.67	0.44

The estimated fishing mortality rates are given in Table 10. The population number at age estimates also obtained from this calculation are given in Table 11. The mean F for ages 4 and older (weighted by population numbers at age) increased from 0.23 in 1958 to 0.50 by 1965. A further peak in F occurred in 1968 (0.57). Lower values in 1969 to 1971 were followed by high F's of 0.60 in 1972 and 0.67 in 1973. F-values for ages greater than age 4 were considerably higher than these means. F of 3-year-olds ranged from 0.04 to 0.25. F of 2-year-olds was negligible until 1963 when it reached 0.16, was low in the mid-1960's, increasing again in 1971 and 1972 to F = 0.12.

Table 11. Cod in Subdiv. 4Vs and Div. 4W: estimated population numbers X 10⁻⁶

Age	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
1	104.1	92.9	99.9	72.8	109.4	126.8	122.3	129.8	146.5	114.7	73.0	82.0	73.5	99.5	93.1	(85.0)	(85.0)
2	91.3	85.2	76.0	81.8	59.6	89.2	102.2	98.9	104.9	119.0	93.8	58.9	66.7	59.8	80.7	75.4	69.1
3	68.2	74.7	69.8	62.2	66.9	46.1	62.5	75.6	72.2	79.8	95.6	71.2	45.1	51.4	43.5	58.6	57.4
4	38.5	53.3	58.9	50.8	47.9	51.1	29.5	43.1	50.8	49.8	61.0	68.3	54.7	31.9	36.1	28.3	37.9
5	23.1	28.3	35.6	42.7	32.9	30.2	32.0	17.1	25.1	30.2	33.8	34.9	44.1	31.9	18.8	18.5	17.0
6	17.8	16.6	15.2	23.1	26.5	21.3	15.3	15.9	9.5	11.3	16.2	13.9	19.5	23.9	18.5	7.0	6.6
7	5.4	11.2	7.7	8.4	12.9	14.5	12.5	8.3	7.4	3.7	5.4	5.8	5.9	11.8	10.3	7.2	2.3
8	3.6	2.9	5.2	3.8	4.2	8.1	7.5	7.7	3.9	3.1	1.7	1.2	2.8	3.0	5.0	5.3	3.2
9	4.3	1.6	1.1	2.6	1.4	1.2	4.6	4.0	2.2	1.8	1.5	0.6	0.6	1.6	0.8	2.4	1.0
10	1.7	1.7	0.5	0.6	1.0	0.5	0.7	2.9	1.4	1.0	0.9	0.4	0.3	0.2	0.9	0.3	0.9
11	0.9	0.6	0.4	0.3	0.4	0.4	0.3	0.3	0.9	0.7	0.3	0.4	0.3	0.2	0.1	0.3	-
Total 4+	95.3	116.2	124.6	132.3	127.2	127.3	102.4	99.3	101.2	101.6	120.8	125.5	128.2	104.5	90.5	69.3	68.4
Total	358.9	369.0	370.3	349.1	363.1	389.4	389.4	403.6	424.8	415.1	383.2	337.6	313.5	315.2	307.8	(288.3)	(279.9)

POPULATION SIZE FROM COHORT ANALYSIS

Population estimates of cod (age 1 and older) increased from 359 million fish in 1958 to 425 million fish in 1966, then decline steadily to 280 million by 1974 (Table 11). Estimates for cod (age 4 and older) increased from 95 million in 1958 to 132 million in 1961. This is followed by a decline through 1965 (99 million) and then a second increase to 128 million by 1970. Subsequent to 1970 a substantial decline occurs to 68 million by 1974.

The data imply that there was a six-year period (1962-67), when the strength of year-classes at age 1 (i.e. the 1961-66 year-classes) was over 100 million fish. The average strength was 125 million with the strongest year-class (1965) being 146.5 million fish. The subsequent five year-classes, those of 1967 to 1971, were all poorer, averaging 84 million fish.

Comparing estimated changes in population from cohort analysis with changes in abundance estimated from Spanish catch per effort data (Table 4), there are apparent inconsistencies. The high catch rates in 1968 should be reflected by a substantial increase in population estimates of fish age 3 and older. While some increase is shown in the population estimates, the increased catches of 1968 are reflected to a large extent as an increase in mortality (Table 10).

It is apparent that the demands placed on the sampling data were too great, and it has not been possible to obtain sufficient resolution to allow detailed interpretation of historical events. It is likely that an extremely strong year-class entered the Spanish fishery in 1968, most likely that of 1965. This is substantiated by the fact that the Canadian fishery, which was based largely on ages 4 and 5 fish, did not show an increase in catch rates (Halliday, 1972). In the cohort analysis, the strength of this year-class has been spread over a number of adjacent year-classes. It is likely, then, that there has been considerably more fluctuation in year-class strength than suggested by this analysis.

In the 1970 to 1974 period sampling coverage was substantially improved over that of the 1960's. It is encouraging that, in this period, Spanish catch rates and cohort analysis are in agreement, but it is unfortunate that they both indicate that there has been a substantial decline in population abundance.

AGE AT RECRUITMENT

The selection at age estimated from the fishing mortalities calculated by cohort analysis for 1972 and 1973 are given above. Due to the quite different selection patterns of the major fishery components, these data give an asymmetrical selection ogive. The mean selection age was estimated graphically by equalization of the areas under the lower and above the upper parts of the curve (e.g., Gulland, 1969), giving a mean selection age of 3.5 yrs. Similar calculations for the period 1969 to 1971 gave a value of 3.95 yrs.

DISCUSSION

Both Spanish commercial catch rates and cohort analysis indicate that there has been a substantial decline in stock abundance in the 1970's. There also appears to have been a decrease in average recruitment during this period.

The mean age at recruitment decreased between 1969-71 and 1972-73 from almost 4.0 years to 3.5 years. F associated with maximum yield per recruit at a mean selection age of 3.5 years is $F_{max} = 0.34$ for Subdiv. 4Vs and $F_{max} = 0.30$ for Div. 4W. This contrasts with the calculated mortality on fully recruited age-groups (age 5+) in 1972-73 of $F = 0.80$. The 1969-71 mean selection age of 4.0 years is associated with $F_{max} = 0.40$ for Subdiv. 4Vs, and $F_{max} = 0.36$ for Div. 4W, while the average F in 1969-71 was 0.55 (ages 6+). Thus, the stocks have been exploited at levels above F_{max} for at least the last six years. With the 1972-73 selection pattern, a reduction in effort of approximately 60% is required to reduce mortality of F_{max} . A long-term increase in yield per recruit of approximately 10% could be anticipated. A reduction in the number of small fish caught, if this increased the mean selection age from 3.5 years to 4.5 years, could increase yield per recruit by a further 10% and require a less severe reduction in effort.

It has not as yet been possible to utilize research vessel survey data to predict likely recruitment success. It appears from cohort analysis, for which the most recent years are likely to be moderately reliable, that recent recruitment has ranged from about 73 million to 100 million fish at age 1 (Table 11). It is assumed in Table 11 that the 1972 and 1973 year-classes are also of that order of magnitude (85 million fish). The less reliable long-term (1957-72 year-class) average from cohort analysis is 103 million fish.

Catch projections were performed, using the 1972-73 selection at age and the following mean weights at age which are those observed in 1974 catches:

Age	\bar{W} (kg)	Age	\bar{W} (kg)	Age	\bar{W} (kg)
1	0.14	5	1.61	9	4.06
2	0.31	6	2.11	10	4.71
3	0.70	7	2.70	11	5.25
4	1.08	8	3.60	12	5.55

Yields from Subdiv. 4Vs and Div. 4W have, on average over the last 17 years, come almost equally from the two divisions. Research surveys over the last five years also indicate that, on the average, the biomass of cod in Subdiv. 4Vs and Div. 4W is similar. Thus, an unweighted average of F_{max} for the two divisions is taken as a management objective. This implies $F_{max} = 0.32$ for the selection pattern of 1972-73 and $F_{max} = 0.38$ for that of 1969-71. A value of $F_{max} = 0.35$ is chosen as representative of average conditions over the last six years and is used as 1976 management objective, assuming that the objective is to maximise yield per recruit.

An alternative objective is to set F at some value less than F_{max} , resulting in some loss of yield but also reductions in the cost of fishing. Thus, the implications of setting F at $F_{0.1}$, which in this case is about $F = 0.20$, is also investigated.

The 1975 TAC for the cod stock in Subdiv. 4Vs and Div. 4W is 60,000 tons. If the strength of 1972 and subsequent year-class are similar to the recent average of 85 million at age 1, the 1975 TAC will generate an $F = 0.80$ (Table 12). If these year-classes approximate the long-term average of 103 million fish, the F in 1975 is 0.75.

Table 12. Subdiv. 4Vs and Div. 4W: Implications of management options for 1976.

Recruitment for 1972 and subsequent year-classes	1975 F	1976 F	1976 catch (mt)	Long-term catch (mt)
85 X 10 ⁶	0.80	0.35	28,000	51,000
		0.20	17,000	46,000
103 X 10 ⁶	0.75	0.35	31,000	62,000
		0.20	19,000	56,000

The implications for 1976 of these two recruitment assumptions are summarized in Table 12. For the lower, fishing at F_{max} in 1976 would yield 28,000 tons; for the higher, the yield would be 31,000 tons. The long-term catches fishing at F_{max} are 51,000 tons and 62,000 tons, depending on recruitment assumptions. If the management decision is taken to reduce fishing to $F_{0.1}$ in 1976, the appropriate catch is 17,000-19,000 tons. The long-term effects of fishing at $F_{0.1}$ are to reduce potential yields by 10%, but the effort required to harvest these lesser yields would be approximately 40% less than required to fish at F_{max} .

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Effects of Diurnal Variation in Availability upon Estimation of Redfish Numbers and Biomass from Stratified-Random Bottom Trawl Surveys¹

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ABSTRACT

The effects of diurnal variation in availability of redfish to the otter trawl upon estimation of redfish numbers and biomass are assessed based on replicated day-night fishing. More than three times as many redfish were caught per day (1,329) than per night (400) standard replicated set. There was a significant four-fold difference in stratified mean weight of redfish caught in replicated day and night sets (281.4 versus 70.6 kg) and an apparent differential diurnal migration off bottom with size (age), with proportionately fewer of the intermediate-sized (22-30 cm) and intermediate-age (8-14) fish being caught at night than at day. The consistent and substantial differences in mean numbers and weights of redfish caught per standard day and night sets invalidate, for species exhibiting pronounced diurnal variations in availability, estimates of numbers and biomass derived from stratified-random 24-hour bottom trawling. It is suggested that estimates of population numbers and biomass for such species should be based only on stations fished during daylight hours.

INTRODUCTION

In recent years stratified-random sampling has been increasingly accepted as a primary tool for assessing relative abundance of demersal stocks of fish. Research vessel surveys by the Newfoundland Biological Station up to 1971 were based on the standard line method of surveying as described by Pinhorn (MS 1971). Since 1971, surveys to the Grand Bank and St. Pierre Bank areas have utilized the stratified-random method of surveying as described in Grosslein and Pinhorn (MS 1971). Pinhorn and Pitt (MS 1974) have presented the results of these surveys for the 1971-73 period. The emphasis in these surveys has been placed upon depths normally frequented by cod, haddock, American plaice and yellowtail flounder, with by far the bulk of the fishing sets occurring at depths of less than 150 fathoms. Some results have been presented for redfish (Pinhorn and Pitt, MS 1974), but it has been realized that, to a large extent, these surveys have only sampled a small fraction of the redfish populations.

In attempting to extend these surveys to adequately sample redfish as well, consideration had to be given to the well-known diurnal vertical migrations of redfish as documented by Steele (1957), Konstantinov and Scherbino (1958), Templeman (1959) and Sandeman (MS 1969). The extent of such vertical migrations has been dramatized by the recent development of a midwater trawl fishery for redfish in the Gulf of St. Lawrence and, to a lesser extent, in Division 3P. In 1973, approximately 30% of the redfish catch in Div. 3P was taken by midwater trawl.

This paper presents the results of a special stratified-random otter trawl survey of Subdivision 3Ps, undertaken in June 1974 with comparative day-night fishing to assess the effects of diurnal variation in availability of *mentella*-type redfish² to the otter trawl upon estimation of redfish numbers and biomass, and examines the implications for redfish abundance estimation.

¹ Submitted to the 1975 Annual Meeting as Res. Doc. 75/45.

² In this paper *mentella*-type redfish includes both the true *Sebastes mentella* (Travin) and the North American form of sharp-beaked redfish, *Sebastes fasciatus* (Storer).

MATERIALS AND METHODS

This study was undertaken during a June 1974 cruise by the Research Vessel A.T. Cameron to Subdiv. 3Ps with comparative day-night fishing at depths ranging from 101 to 300 fathoms. The stratification scheme previously reported for Subdiv. 3Ps (Pinhorn, 1972) was modified such that strata were drawn up on the basis of the following depth contours: 101-150, 151-200, 201-300 and 301-400 fathoms (Fig. 1).

In eleven of the sixteen strata fished, a minimum of two (and generally more) randomly selected stations were fished both during the day and the night. Sets designated as day sets were generally fished during the period from about one hour after sunrise to about one hour before sunset, night sets during the period from about one hour after sunset to about one hour before sunrise.

All tows with the No. 41-5 otter trawl, with codend lined with 1/4" to 1-1/8" nylon mesh, were 30 minutes in duration.

Where time permitted, additional unreplicated day sets were fished at other randomly selected stations within a particular stratum. Because of operational requirements, it was not possible to carry out comparative day-night fishing in all strata. Five of the sixteen strata fished were fished only during daylight hours. Results for these strata are included in the overall estimates based on day sets but not in the day-night comparisons which are based only on stations where sets were replicated.

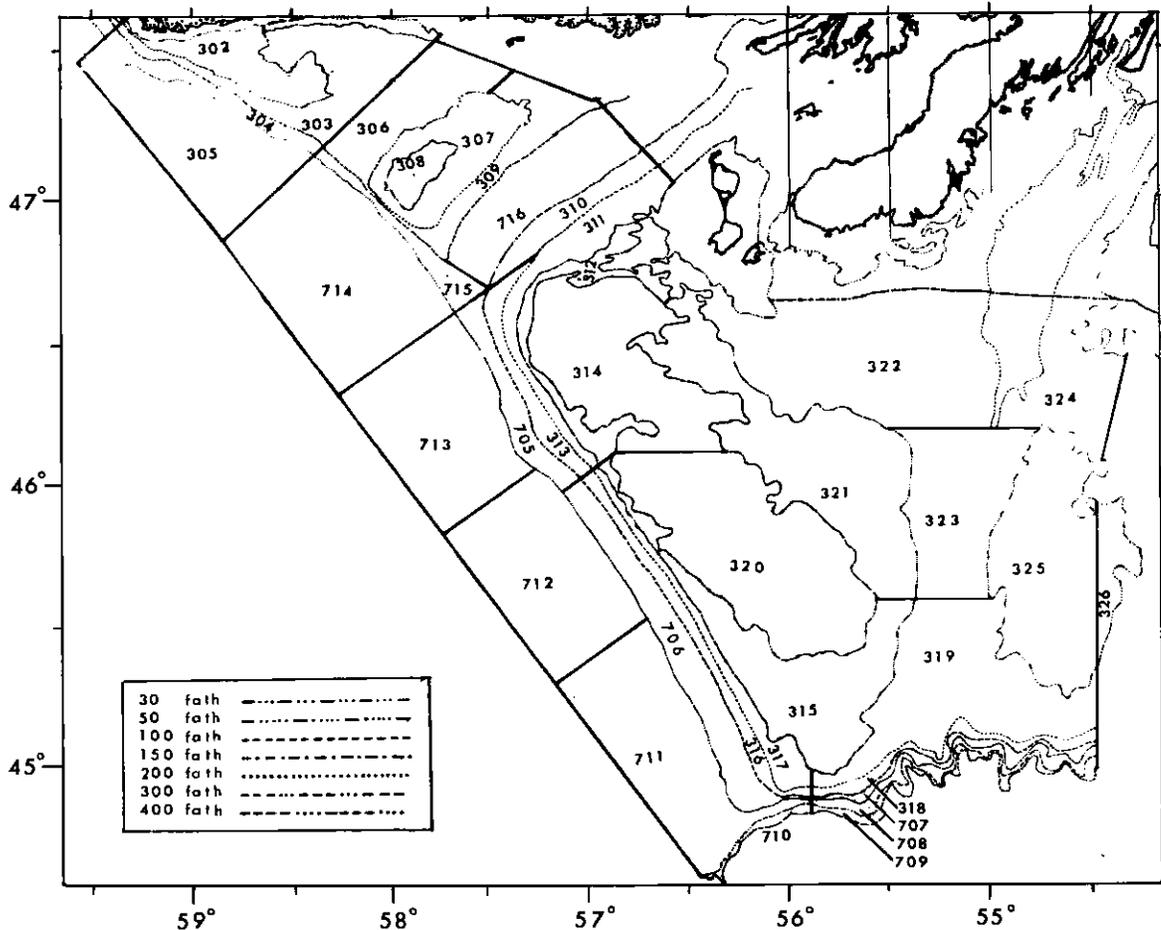


Fig. 1. Map showing the strata fished on a stratified-random survey of Subdiv. 3Ps during R/V A. T. Cameron Cruise 224, June 1974.

RESULTS

Comparison of Day-Night Numbers and Biomass Estimates

Stratified mean numbers and weights (kg) per standard set and relevant statistics for replicated day-night sets are presented in Tables 1 and 2 for selected demersal species. Stratified mean numbers of *mentella*-type redfish caught per standard set for day and night replicates are depicted in Fig. 2.

There was a more than three-fold difference in stratified mean numbers of redfish caught during replicated day and night fishing (1,328.6 versus 399.3; Table 1). The mean number for replicated daylight sets was outside of the 95% confidence limits for the stratified mean number caught at night and similarly the mean number caught at night was outside of the 95% confidence limits for the replicated day sets. The 95% confidence limits for the estimated mean number per replicated day set were considerably narrower ($\pm 40\%$ of the mean) than those for the estimated mean number per replicated night set ($\pm 177\%$ of the mean). For all strata in which comparative day-night fishing was conducted the mean number of redfish caught in replicated day sets was substantially larger than the mean number caught in the replicated night sets (Fig. 2).

Table 1. Stratified mean number per standard set and relevant statistics for replicated day-night sets, A.T. Cameron Cruise 224, June 1974, in ICNAF Subdiv. 3Ps.

Species	Type of set ¹	Mean	Variance	Standard deviation	Coefficient of variation	95% Limits	
						Upper	Lower
Redfish	Day-replicated	1328.6	48312.00	219.80	0.17	1875.9	781.30
	Night-replicated	399.3	6934.00	83.30	0.21	1107.9	-309.30
Cod	Day-replicated	2.5	1.80	1.30	0.54	6.7	-1.80
	Night-replicated	7.8	18.40	4.30	0.55	19.5	-4.00
Haddock	Day-replicated	1.8	1.10	1.10	0.58	4.6	-1.00
	Night-replicated	1.4	0.41	0.64	0.46	3.2	-0.39
Plaice	Day-replicated	4.3	0.95	0.98	0.23	6.9	1.60
	Night-replicated	2.2	0.19	0.43	0.20	3.3	1.10
Witch	Day-replicated	15.4	8.70	3.00	0.19	22.4	8.30
	Night-replicated	27.5	55.20	7.40	0.27	45.9	9.20

¹ Strata used for diurnal comparison: 306, 309, 310, 313, 316, 318, 705, 706, 707, 715, 716.

Table 2. Stratified mean weights (kg) per standard set and relevant statistics for replicated day-night sets, A.T. Cameron Cruise 224, June 1974, ICNAF Subdiv. 3Ps.

Species	Type of set	Mean	Variance	Standard deviation	Coefficient of variation	95% Limits	
						Upper	Lower
Redfish	Day-replicated	281.40	1746.10	41.80	0.15	386.70	176.10
	Night-replicated	70.60	103.10	10.20	0.14	104.00	37.10
Cod	Day-replicated	1.80	0.52	0.72	0.39	3.60	0.03
	Night-replicated	3.30	2.60	1.60	0.50	7.80	-1.30
Haddock	Day-replicated	1.40	0.57	0.75	0.54	3.50	-0.71
	Night-replicated	1.00	0.21	0.46	0.46	2.20	-0.15
Plaice	Day-replicated	1.20	0.10	0.32	0.27	2.00	0.33
	Night-replicated	0.56	0.01	0.12	0.21	0.86	0.26
Witch	Day-replicated	4.60	0.98	0.99	0.21	7.00	2.30
	Night-replicated	8.30	3.70	1.90	0.23	12.70	3.80

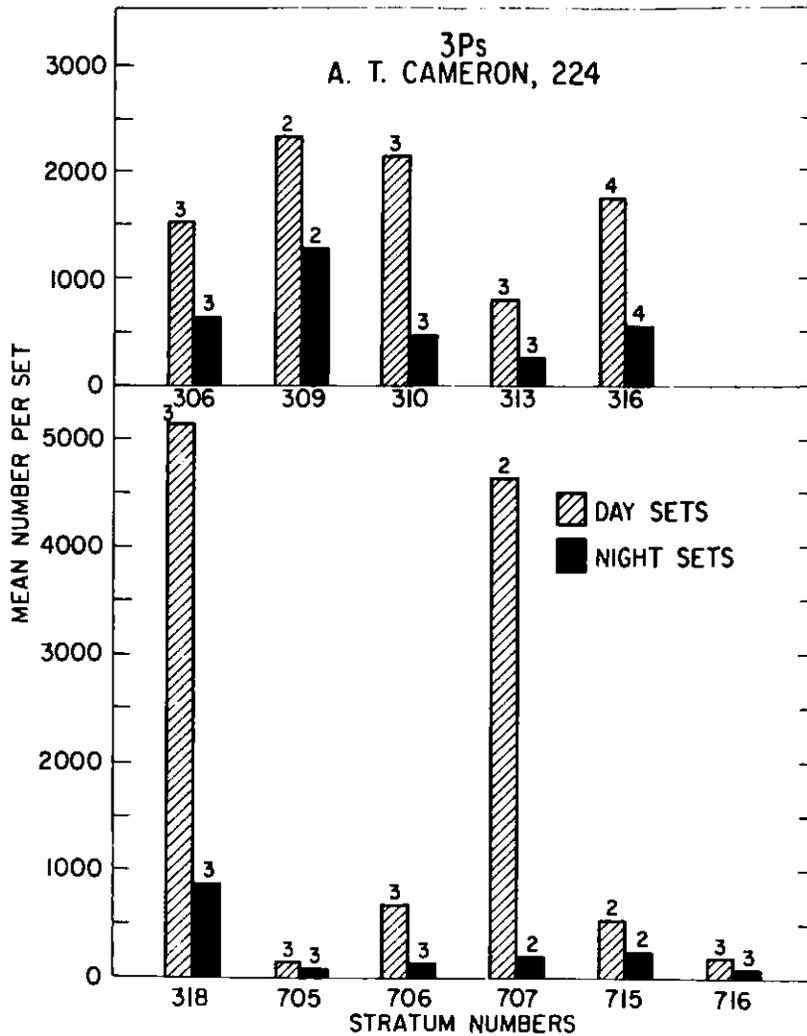


Fig. 2. Mean numbers of *mentella*-type redfish caught per standard day and night set for each stratum in which comparative day-night fishing was conducted. (The numbers over each column represent the number of replicate sets fished in each stratum.)

There was a significant four-fold difference in stratified mean weight of redfish caught in replicated day-night sets (281.4 versus 70.6 kg; Table 2). The 95% confidence limits for the two means do not overlap. The confidence limits for the estimated mean weight per replicated day set were slightly narrower ($\pm 37\%$ of the mean) than those for the estimated mean weight per replicated night set ($\pm 47\%$ of the mean).

Only small numbers of other demersal species were caught on this cruise (Table 1); hence, no meaningful conclusions could be drawn about the effects of diurnal variation in availability of these species to the otter trawl.

A comparison of these results with estimates obtained from numbers and weights caught during day and night unreplicated sets in two selected strata 306 and 309¹ (Tables 3 and 4) on an earlier 1974 April cruise indicates a similar trend but differences for just these two strata were much less pronounced than those obtained when a greater range and number of strata were fished on the June cruise.

¹ The boundaries of strata 306 and 309 were altered between the April and June cruises.

Table 3. Stratified mean numbers per standard set and relevant statistics for unreplicated day and night sets, Strata 306 and 309¹, A.T. Cameron Cruise 221, April 1974, ICNAF Subdiv. 3Ps.

Species	Type of set	Mean	Variance	Standard deviation	Coefficient of variation	95% Limits	
						Upper	Lower
Redfish	Day-unreplicated	811.30	99157.00	314.90	0.39	1812.70	-190.00
	Night-unreplicated	429.40	48676.00	220.60	0.51	1104.50	-245.80
Cod	Day-unreplicated	6.10	3.20	1.80	0.29	10.60	1.60
	Night-unreplicated	2.20	1.30	1.10	0.49	5.40	-0.85
Haddock	Day-unreplicated	0.40	0.04	0.20	0.50	0.91	-0.12
	Night-unreplicated	0.10	0.01	0.10	1.00	0.43	-0.22
Plaice	Day-unreplicated	0.41	0.17	0.41	1.00	1.70	-0.90
	Night-unreplicated	1.40	0.46	0.68	0.50	3.20	-0.52
Witch	Day-unreplicated	31.10	39.00	6.20	0.20	46.50	15.80
	Night-unreplicated	25.90	30.30	5.50	0.21	40.90	10.80

¹ Boundaries of Strata 306 and 309 were altered between the April and June cruises.

Table 4. Stratified mean weight (kg) per standard set and relevant statistics for unreplicated day-night sets, Strata 306 and 309, A.T. Cameron Cruise 221, April 1974, ICNAF Subdiv. 3Ps.

Species	Type of set	Mean	Variance	Standard deviation	Coefficient of variation	95% Limits	
						Upper	Lower
Redfish	Day-unreplicated	88.40	685.00	26.20	0.30	169.50	7.30
	Night-unreplicated	46.40	302.10	17.40	0.37	100.90	-8.20
Cod	Day-unreplicated	17.80	17.90	4.20	0.24	28.30	7.30
	Night-unreplicated	3.00	1.40	1.20	0.40	6.30	-0.20
Haddock	Day-unreplicated	0.47	0.11	0.33	0.69	1.50	-0.54
	Night-unreplicated	0.44	0.20	0.44	1.00	1.90	-0.97
Plaice	Day-unreplicated	0.01	0.00	0.01	0.94	0.04	-0.02
	Night-unreplicated	0.26	0.03	0.17	0.64	0.78	-0.25
Witch	Day-unreplicated	11.30	3.90	2.00	0.17	16.20	6.30
	Night-unreplicated	9.40	4.90	2.20	0.24	15.70	3.10

Size and Age Composition

The length distribution of both male and female redfish in standard day and night sets (Fig. 3) were significantly different at the 1% level (Kolmogorov-Smirnov two-sample test). A comparison of the percentage length compositions (Fig. 4) reveals that the redfish caught during a standard night set were proportionately smaller than those caught during a standard day set at the same stations. This trend was evident in the majority of individual strata in which comparative day-night fishing was conducted.

A plot of the numbers caught per standard night set as a proportion of the numbers caught per standard day set at each length interval (Fig. 5A) suggests a differential rate of diurnal migration off bottom with size. Proportionately fewer of the intermediate-sized fish (22-30 cm) remained on bottom at night.

An examination of the night-to-day ratios of numbers caught at each age (Fig. 5B and 6) suggests, as might be expected from the trend with size, a differential diurnal migration rate with age, with proportionately fewer redfish of intermediate age (8 to 14 years) being caught at night than at day. The diurnal migration rate of 8- to 14-year-old redfish is proportionately greater than that for younger and older fish.

From the ratio of night-to-day catches per standard set plotted against numbers caught per standard day set (Fig. 7), it would appear that there is no significant relationship between daytime abundance and proportional movement off bottom during the night.

There was no significant difference in the sex ratios of the numbers caught per standard day and night set.

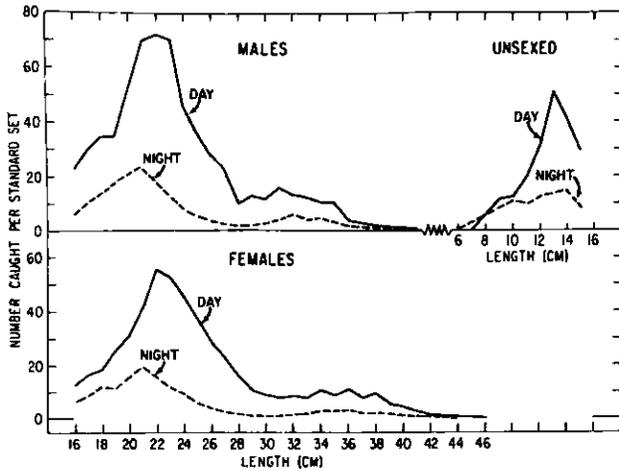


Fig. 3. Length distribution of *mentella*-type redfish per standard day and night sets (based on replicated fishing).

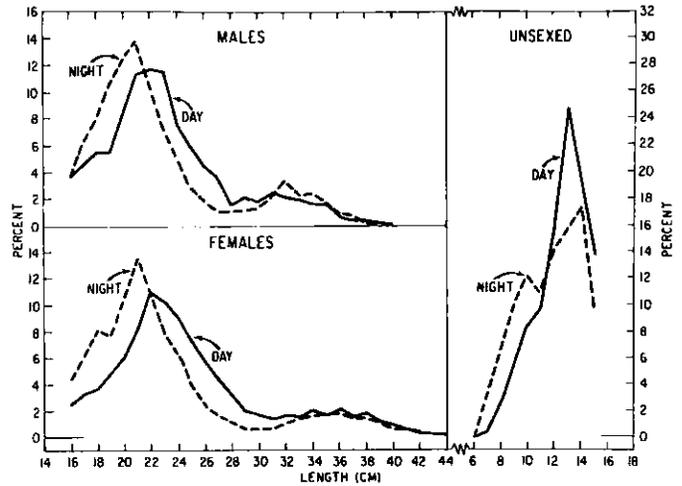


Fig. 4. Percentage length composition of *mentella*-type redfish per standard day and night set (based on replicated fishing).

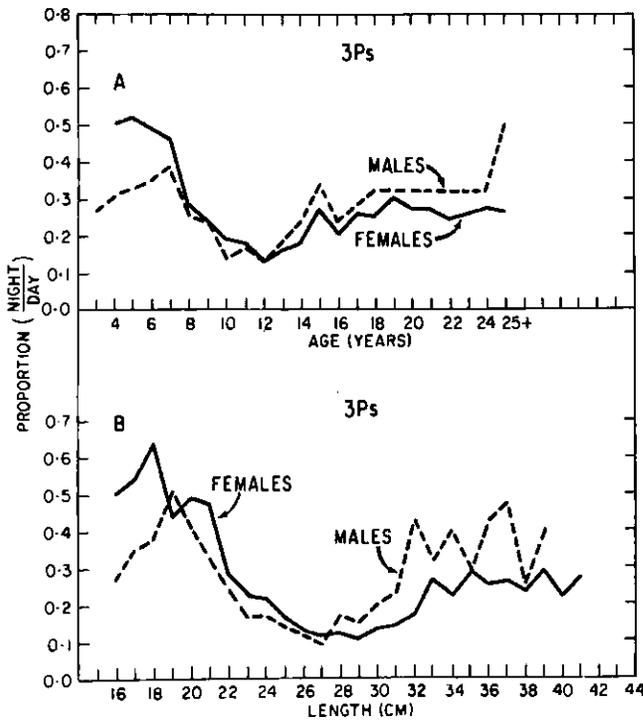


Fig. 5. Numbers of redfish caught per standard night set as a proportion of numbers caught per standard day set in relation to length (A) and age (B).

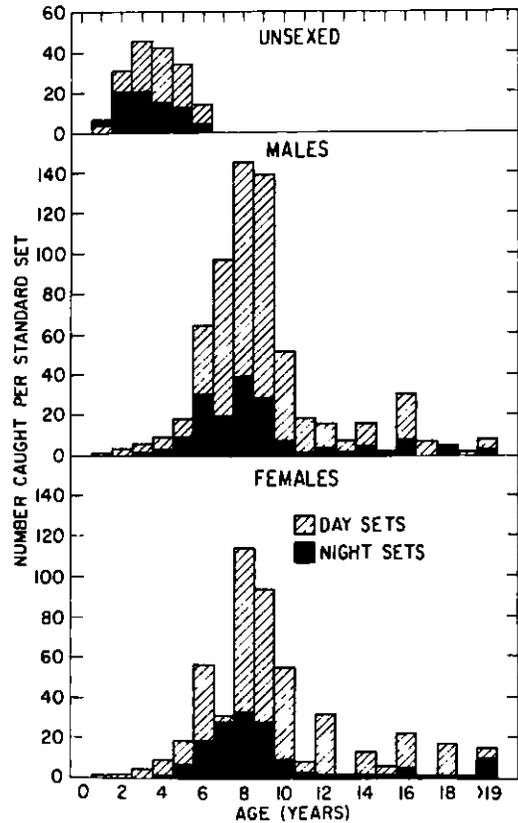


Fig. 6. Numbers of redfish caught at each age per standard day and night set (based on replicated fishing).

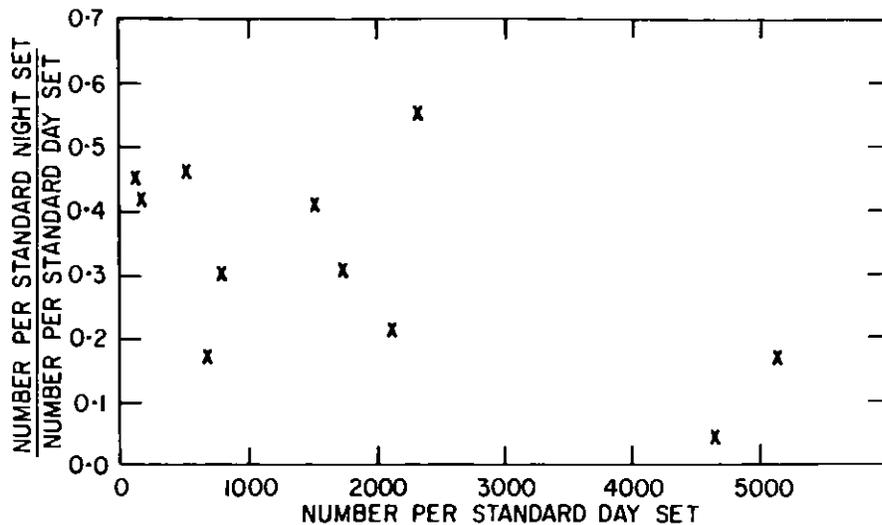


Fig. 7. Ratio of day-to-night numbers of redfish caught per standard set plotted against numbers caught per standard day set.

Overall Estimates from Day Sets

Stratified mean numbers and weights per standard day set and relevant statistics, based on the total daylight sets in all sixteen strata surveyed, are given in Table 5. Overall mean number per standard day set was 854.8 and mean weight 219.3 kg. This is considerably less than the mean numbers per set in the 1973 and 1965 redfish research surveys of Subdiv. 3Ps, using the standard line survey method, of 1,266 and 2,629 fish respectively. For comparison, the 1965 and 1973 surveys were post-stratified, using the strata boundaries of Fig. 1, and estimates derived for the six strata fished in all three years. Stratified mean number per unit for these strata in 1974 (1,998.3) was about 20% higher than the post-stratified mean number per unit for the 1973 survey (1,667.5); both were considerably less than the post-stratified mean number per unit for the 1965 survey (3,189.6).

Table 5. Stratified mean numbers and weights (kg) per standard set and relevant statistics for total day sets in all strata, A.T. Cameron Cruise 224, June 1974, ICNAF Subdiv. 3Ps.

	Mean	Variance	Standard deviation	Coefficient of variation	Estimated total for all strata fished	95% Limits	
						Upper	Lower
Number	854.8	18499.7	136.0	0.16	449 × 10 ⁶	592 × 10 ⁶	306 × 10 ⁶
Weight (kg)	219.3	761.2	27.6	0.13	115 × 10 ⁶	144 × 10 ⁶	86 × 10 ⁶

Estimated numbers of redfish in Subdiv. 3Ps were 449 million fish and the estimated minimum trawlable biomass was 115,000 metric tons. The 95% confidence limits for the numbers and biomass estimates were within ±32% and ±25% of the respective means.

Greatest mean numbers and mean weights per standard day set were obtained in the 101-150 fathom strata, with centers of greatest abundance in the Hermitage Channel immediately east of Burgeo Bank and on the southeastern edge of St. Pierre Bank (Fig. 8). Mean numbers and weights per standard day set were considerably lower in the 151-200 fathom and 201-300 fathom strata, with the exception of the southeasternmost strata (318, 707 and 708) where redfish abundance was high at all depths surveyed.

Bottom temperatures at the stations fished ranged from 4.8 to 8.0°C, the upper part of the range of preferred temperatures for redfish (Templeman, 1959). Bottom temperature did not appear to be the principal factor determining centers of redfish abundance within the survey area, although at temperatures of less than 5.5°C the numbers caught were invariably low (Fig. 9).

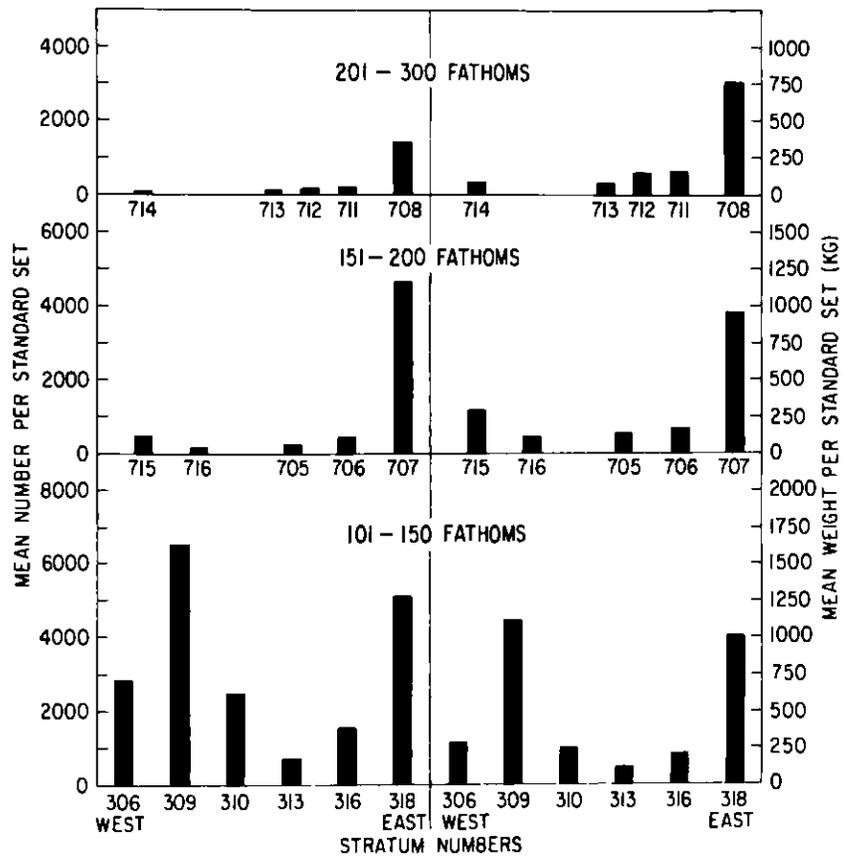


Fig. 8. Mean numbers and weights per standard day set - all strata (based on total day sets fished).

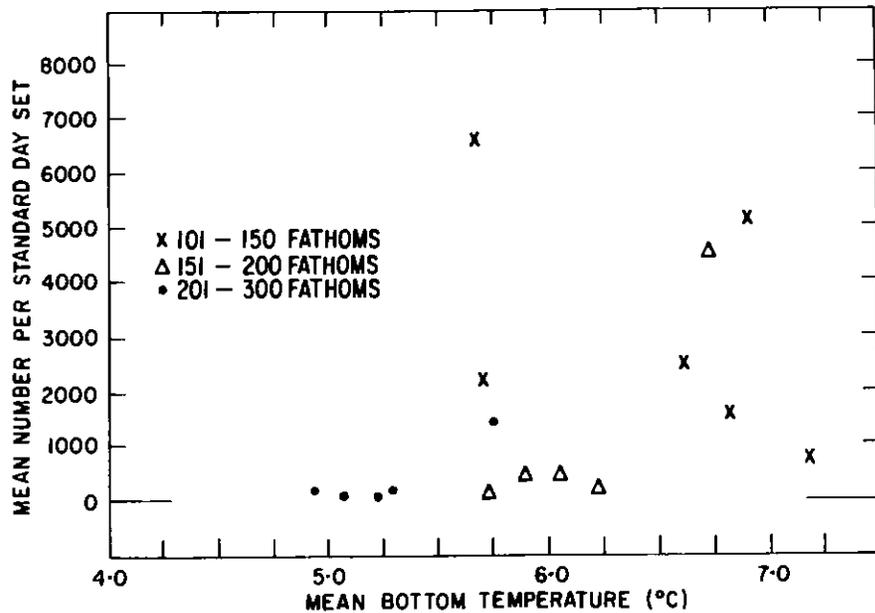


Fig. 9. Mean number of redfish per standard day set plotted against mean bottom temperature in each stratum.

Eight- and 9-year-old redfish of the 1966 and 1965 year-classes accounted for 34% of the redfish caught in standard day sets; 60% were between the ages of 6 and 10 (Fig. 10). Since relatively small and young redfish (16-25 cm and 6-10 years old) were predominant in the survey catches (Fig. 10), it would be expected from the well-known differential depth distribution of redfish with size (age) that the shallower strata (101-150 fathoms) fished would have the largest concentrations of redfish.

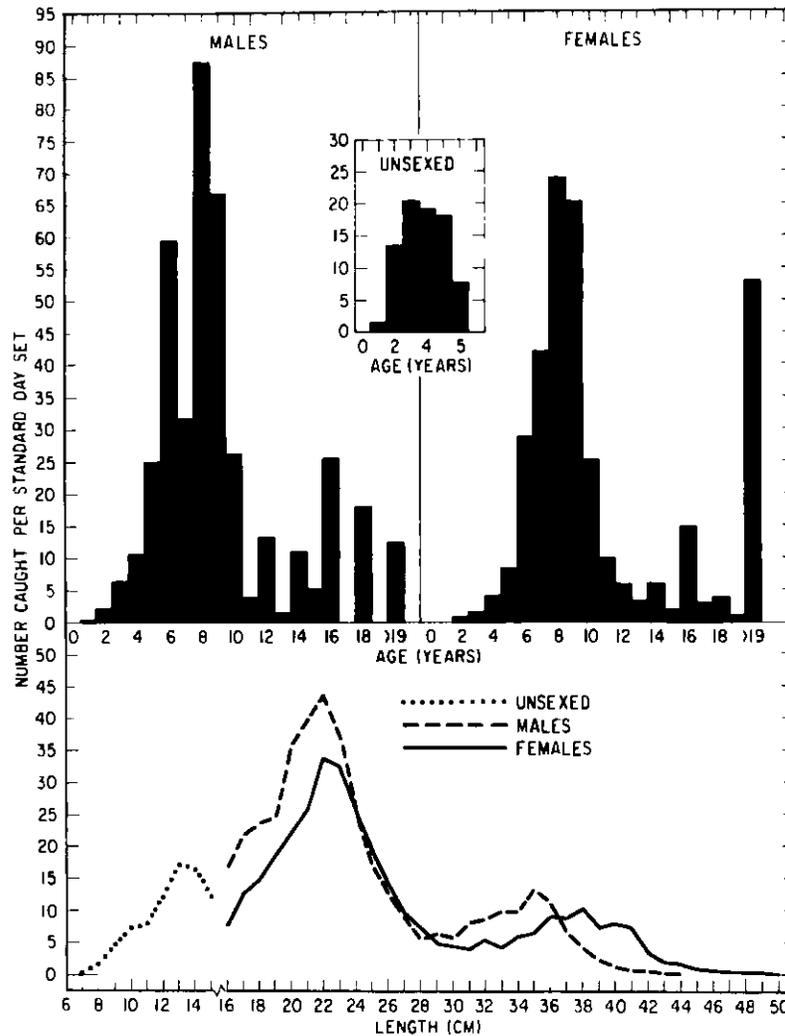


Fig. 10. Numbers caught at each length and age per standard day set - all strata and all day sets combined.

DISCUSSION AND CONCLUSIONS

The results of the comparative day-night fishing reveal consistent and substantial differences in mean numbers and weights of redfish caught per standard day and night sets for all strata in which replicated day-night fishing was performed. The resulting differences in estimates of redfish numbers and weights derived from the replicated day and night fishing are substantial enough to cast serious doubt upon any estimates obtained by random 24-hour fishing, as might have been expected from previous knowledge of diurnal variation in availability of redfish to bottom trawls.

To date most of the stratified-random bottom trawl surveys in the Northwest Atlantic have been predicted on the assumption that such effects will average out over long periods of 24-hour fishing at randomly selected stations within predetermined strata. An examination of trawling records of the Newfoundland Biological Station spring stratified-random

bottom trawl surveys in Subdiv. 3Ps during 1972-73, with classification of fishing sets by time of day, revealed an uneven diurnal distribution of fishing sets within particular strata (Fig. 11).

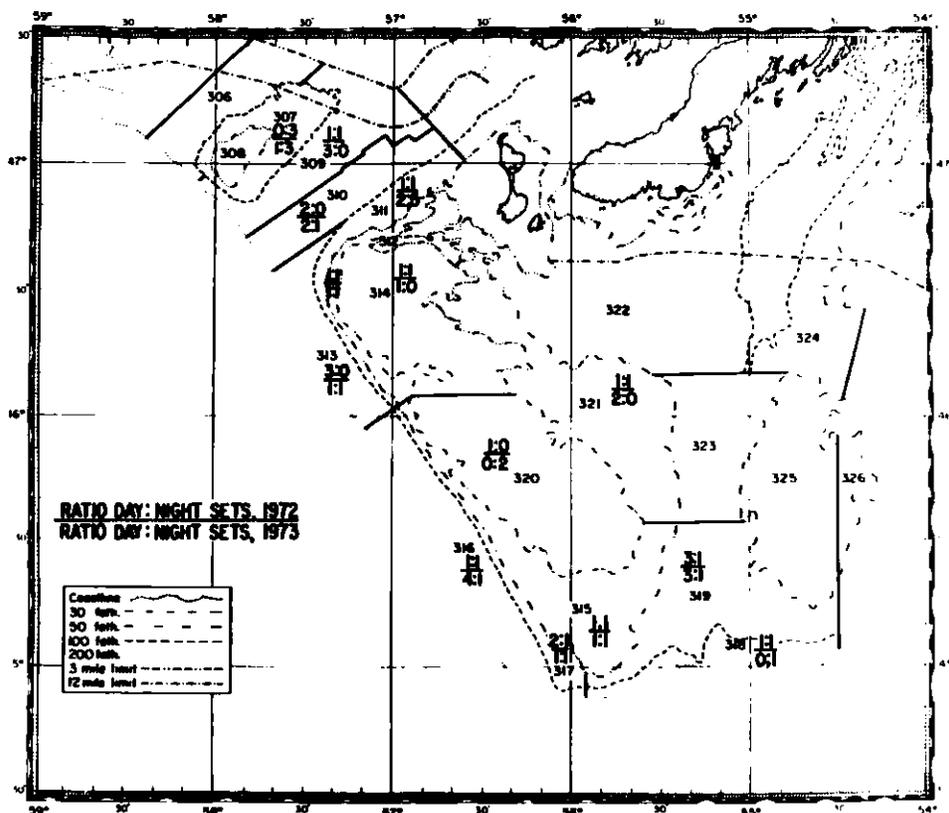


Fig. 11. Ratio of day-to-night sets in each stratum fished on stratified-random surveys in Subdiv. 3Ps, 1972 and 1973. (In each stratum, the upper figures represent the ratio of day-to-night sets in the 1972 cruise; the lower figures represent the ratio of day-to-night sets in the 1973 cruise.)

Depending upon the actual distribution of fish among the strata during any particular survey cruise, estimates of numbers and biomass for any species exhibiting pronounced diurnal variations in availability could be seriously biased by year-to-year or cruise-to-cruise changes in fishing pattern and non-proportional allocation of day and night sets among strata.

For this reason, unless reliable and consistent conversion factors between day-night catches of such species can be derived, a feat not possible to date¹, estimates of numbers and biomass for redfish and other species exhibiting pronounced diurnal variations in availability to the survey gear should, for bottom trawl surveys, be derived only from stations fished during daylight hours. Because of the necessity to maximize the number of usable fishing sets per stratum, these considerations further suggest that for maximum efficiency stratified-random bottom trawl surveys aimed at abundance estimation for such species should be conducted, insofar as circumstances permit, during periods when daylight hours are close to maximal.

We were fortunate in this respect that the survey reported here was conducted during the latter half of June and consequently sufficient numbers of stations were fished during daylight hours to enable us to derive estimates of redfish numbers and biomass from the daylight portion of the survey. The relatively narrow confidence limits ($\pm 32\%$ for the estimate of numbers and $\pm 25\%$ for the estimate of weights; Table 5) are as good as any obtained in demersal fish surveys conducted by the Newfoundland Biological Station and better than the precision of $\pm 50\%$ generally attainable in such surveys (Grosslein, MS 1971)

¹ In this study ratios of day-to-night catches in individual strata ranged from 1.8 to 24.7 for numbers and from 1.6 to 28.8 for weights.

For redfish there is quite a marked gain in precision with stratification according to time of day, with bottom fishing restricted to daylight hours. It appears that estimates based on stratified-random bottom trawling during daylight hours may indeed be useful for assessment of trends in redfish abundance, even though the actual estimates of numbers and biomass must continue to be regarded as minimal until such time as catchability factors can be determined. Scott (MS 1971), in estimating abundance of groundfishes on the Scotian Shelf, used an overall catchability factor of 0.27 for redfish, obtained from Edwards (1968), which was based on component availability, vulnerability and areal/seasonal factors of 0.45, 0.75 and 0.80 respectively. This factor was virtually identical to that used for cod (0.28) in the same study. In view of the probable differences in the degree of diurnal variation in availability of cod and redfish to the otter trawl, these estimates must be regarded as highly subjective.

The results of our study also suggest a differential diurnal variation with size and age in availability of redfish to the otter trawl, with apparently greater proportions of the intermediate sizes and ages moving off bottom during the night. Sandeman (1969), in a detailed study of the diurnal variation in availability of different sizes of redfish during a series of alternate haul mesh selection experiments directed at redfish on the eastern part of the Grand Bank, found that the catchability of redfish varied with size with greater proportions of the smaller redfish being caught than of the larger. Our results indicate a variation with size (age) in the proportion of redfish becoming available to the bottom trawl during the night.

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A Preliminary Assessment of the Redfish, *Sebastes marinus* (L.), in ICNAF Divisions 4VWX

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ABSTRACT

Commercial catch and effort data for the ICNAF Division 4VWX redfish fishery are presented and utilized to calculate maximum sustainable yield and corresponding effort. Estimates of total instantaneous mortality (Z) were obtained from commercial length frequency samples. A yield per recruit analysis was carried out using von Bertalanffy growth parameters derived from 1974 Canadian commercial samples.

The total redfish catch from Div. 4VWX rose from 7,195 metric tons in 1936 to a maximum of 77,142 tons in 1949. Between 1952 and 1970, the total catch fluctuated between 10,000 and 40,000 tons per year. Recently, increased catches by distant water fleets caused a sharp rise in the total catch to 62,381 and 50,300 tons in 1971 and 1972 respectively. This level has subsequently declined to 40,173 tons in 1973 and 32,819 tons in 1974.

Catch curves based on length frequency samples for the period 1971 to 1974 gave an estimated Z of 0.4. Yield per recruit was calculated with an assumed $m = 0.1$. With a length at first capture of 20 cm corresponding to an age of six years, F_{max} was estimated at 0.16 for males and 0.20 for females. Maximum sustainable yield estimates of 43,500 and 32,000 tons were obtained from a Schaefer curve using 8 and 12 year average effort periods.

INTRODUCTION

The redfish in ICNAF Div. 4VWX have been commercially exploited since the mid-1930's. Canadian and USA vessels have traditionally accounted for the greatest share of the catch from this area. In recent years, distant water fleets have increased the catch to a level close to that attained during the period of initial expansion of the fishery.

In this paper, length composition data are presented and estimates of the total mortality rate, and von Bertalanffy growth parameters are given. In addition, a yield per recruit analysis and a generalized production model are presented and used to estimate the fishing mortality maximizing yield per recruit, the maximum sustainable yield, and corresponding fishing effort.

COMMERCIAL FISHERY

The fishery for redfish in ICNAF Div. 4V, 4W, and 4X has been conducted mainly by Canadian and USA vessels. Large catches did not occur until 1936 when 7,195 tons were landed by USA fishermen. Canadian landings were not significant until 1961. Catches by distant water fleets have also contributed to the overall total catch since 1962 (Table 1).

¹ Submitted to the Seventh Special Commission Meeting, September 1975 as Res.Doc. 75/IX/135.

Table 1. Redfish nominal catches in ICNAF Div. 4VWX by country and calendar year (metric tons round).

Year	ICNAF DIV.					COUNTRY										Non-mem. & Others
	4Vn	4Vs	4W	4X	Total	CAN	FRA	FRG	ICE	ITA	JAP	POL	USSR	UK	USA	
1954	-	12,772	4,474	4,686	21,932	1,037	-	-	-	-	-	-	-	-	20,895	-
1955	-	5,223	3,106	1,398	9,727	397	-	-	-	-	-	-	-	-	9,330	-
1956	-	5,641	4,604	6,310	16,555	242	-	-	-	-	-	-	-	-	16,313	-
1957	-	5,499	11,106	3,893	20,498	508	-	-	-	-	-	-	-	-	19,990	-
1958	-	8,131	14,939	9,286	32,356	757	-	-	-	-	-	-	-	-	31,599	-
1959	2,058	5,347	12,400	5,510	25,315	611	-	-	-	-	-	-	-	-	24,704	-
1960	5,889	8,123 ¹	11,127	12,344	37,483	1,171	17	-	-	1	-	-	-	-	36,294	-
1961	4,826	4,170	9,411	13,077	31,484	2,511	4	-	-	-	-	-	9	-	28,960	-
1962	3,271	4,479 ¹	16,173	12,812	36,735	3,388	-	-	-	2	-	-	3,975	-	29,370	-
1963	2,746	6,275 ¹	20,146	9,592	38,759	3,175	-	7	-	-	-	-	12,288	2	23,282	5
1964	2,430	7,697 ¹	6,535	6,244	22,906	3,045	51	427	9	-	-	-	3,659	6	15,641	68
1965	2,867	3,319	7,740	5,652	19,578	4,717	188	19	-	-	-	-	1,571	1	13,082	-
1966	6,888	3,067	16,105	14,776	40,836	10,010	63	-	-	-	-	-	13,943	-	16,679	141
1967	8,852	1,989	2,812	4,591	18,244	9,856	-	-	-	-	-	156	67	3	6,415	1,747
1968	7,730	2,222	1,169	1,982	13,103	7,852	427	-	-	-	-	-	186	-	4,635	3
1969	6,259	10,025	3,695	2,763	22,742	10,750	933	98	-	-	-	6,898	2,152	-	1,142	769
1970	4,246	6,694	16,215	4,424	31,579	15,293	131	-	-	-	968	20	13,218	-	1,949	-
1971	6,954	23,698	19,953	11,776	62,381	29,308	285	-	-	-	1,164	1,260	20,591	-	6,261	3,512
1972	4,525	14,580	22,223	8,972	50,300	21,869	107	-	-	-	2,273	65	11,858	13	12,365	1,750
1973	7,125	11,213	14,709	7,126	40,173	16,488	15	-	-	-	1,747	49	10,601	-	10,751	522
1974	6,947	8,088	11,628	6,156	32,189	15,741	396	40	-	-	170	803	6,696	76	8,897	-

¹ The following catches assigned to Subarea 4 (unknown) or Div. 4V (unknown) assigned to Subdiv. 4Vs as follows: 1960 - 1 ton by Italy; 1962 - 2 tons by Italy, 105 tons by USSR; 1963 - 5 tons by Non-members; 1964 - 68 tons by Non-members.

The period of initial exploitation was complete by 1951 with a maximum catch of 77,142 tons occurring in 1949 (Table 2). This was followed by a longer period extending from 1952 to 1970 which was characterized by lower catches with fluctuations between 10,000 and 40,000 tons per year. Recently, increased catches by distant water fleets, particularly those of USSR and Poland, have caused a sharp rise in the total redfish catch from Div. 4VWX to 62,381 and 50,300 tons in 1971 and 1972, respectively. The total has subsequently declined to 40,173 tons in 1973 and 32,819 tons in 1974¹ (Table 2).

Table 2. Total redfish catch (metric tons), US C/E and estimated total effort (days fished) in ICNAF Div. 4VWX.

Year	Catch	C/E	Effort	Adj C/E	Adj Eff.	Year	Catch	C/E	Effort	Adj C/E	Adj Eff.
1942	2,226	15.4	145	15.4	145	1959	25,313	20.6	1,229	16.5	1,534
1943	3,710	27.4	135	27.4	135	1960	37,483	21.8	1,719	17.0	2,205
1944	4,101	22.2	185	22.2	185	1961	31,484	19.4	1,623	14.7	2,142
1945	21,897	17.8	1,230	17.8	1,230	1962	36,735	18.8	1,954	13.9	2,643
1946	38,520	25.0	1,541	25.0	1,541	1963	38,759	15.0	2,584	10.8	3,589
1947	26,525	18.6	1,426	18.6	1,426	1964	22,906	13.2	1,735	9.2	2,490
1948	64,940	25.8	2,517	25.8	2,517	1965	19,578	21.0	932	14.2	1,379
1949	77,142	19.8	3,896	19.8	3,896	1966	40,836	28.2	1,448	16.6	2,460
1950	59,691	16.8	3,553	16.8	3,553	1967	18,244	21.6	845	13.0	1,403
1951	68,844	19.8	3,477	19.8	3,477	1968	13,103	31.6	415	17.7	740
1952	38,105	15.2	2,507	14.8	2,575	1969	22,742	30.6	743	18.3	1,243
1953	14,128	14.6	968	13.8	1,024	1970	31,579	28.4	1,112	15.3	2,064
1954	21,932	22.0	997	20.3	1,080	1971	62,381	31.0	2,012	18.4	3,390
1955	9,727	17.0	572	15.2	640	1972	50,300	29.4	1,711	16.2	3,105
1956	16,555	22.4	739	19.5	849	1973	40,173	23.4	1,717	12.7	3,163
1957	20,498	22.4	915	18.8	1,090	1974	32,819	22.8	1,439	12.1	2,712
1958	32,356	24.0	1,348	19.8	1,634						

COMMERCIAL LENGTH SAMPLING DATA

Commercial length frequency samples from Div. 4VWX were examined to determine length frequency distributions for the period 1965 to 1974. USSR length frequencies were applied

¹ A total allowable catch of 40,000 tons was in effect under ICNAF regulations for 1974.

to USSR catches for the period 1969 to 1974 but prior to this period, USA sampling data were applied to USSR catches. USA sampling data were used to determine length frequencies of all other countries excluding Canada except for 1969 when Canadian length samples were used as no USA data were available. Canadian sampling data were applied to Canadian catches for the period 1965-1974. USA samples were applied to USA catches except for 1969 when Canadian samples were used.

A length-weight equation as determined from Canadian survey samples from 1970 to 1974 was calculated as follows:

$$\text{Log}_{10} W(\text{gm}) = -1.755 + 2.959 \text{Log}_{10} L(\text{cm}).$$

Average weights for each length group in the commercial fishery were calculated using this equation and used to estimate catch in numbers by 1-cm length groups (Table 3).

Table 3. Estimated numbers ($\times 10^{-3}$) of Div. 4VWX redfish landed by length for all countries combined.

Length (cm)	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
10	-	-	-	-	-	67	-	-	-	-
11	-	-	-	-	-	143	-	-	28	18
12	-	-	-	-	-	150	-	24	61	39
13	-	-	-	-	-	544	259	8	188	114
14	31	21	-	-	-	1,309	786	0	388	245
15	68	66	90	-	-	2,211	918	0	238	150
16	233	161	0	-	-	3,210	2,787	76	475	239
17	354	568	162	7	-	4,956	8,007	61	1,028	545
18	377	1,296	374	27	-	8,913	11,916	262	2,032	896
19	726	1,445	350	40	8	9,286	12,948	439	3,697	1,577
20	975	2,936	1,235	81	19	11,106	10,707	1,037	6,736	3,307
21	2,212	4,018	2,106	79	17	9,368	9,259	2,967	10,489	5,248
22	3,342	6,729	2,198	108	91	8,513	9,664	6,682	13,412	6,500
23	5,273	8,583	2,489	131	231	6,565	13,194	10,354	13,870	7,860
24	7,494	12,238	3,369	157	316	5,423	14,978	14,707	12,716	8,231
25	7,050	13,660	3,300	219	496	3,979	15,753	17,502	13,244	8,773
26	5,976	12,625	2,556	307	563	3,007	14,941	17,195	10,852	7,688
27	5,904	10,484	3,060	507	627	2,919	12,215	14,652	9,580	7,453
28	5,240	9,518	2,785	662	1,688	2,681	10,473	12,894	7,399	6,175
29	4,662	7,951	2,780	1,065	2,556	2,792	9,352	10,218	5,556	5,059
30	3,365	8,002	3,271	1,515	3,776	2,892	8,376	8,416	5,290	4,960
31	2,414	5,468	3,419	1,868	3,570	2,881	6,677	5,890	3,618	3,936
32	1,436	3,595	3,238	2,164	3,937	3,098	6,182	5,141	3,444	3,271
33	1,474	3,065	3,063	1,922	3,566	2,683	5,852	4,150	3,388	2,614
34	1,072	1,908	1,856	1,972	3,437	3,004	6,016	3,577	2,790	2,230
35	991	2,381	1,154	1,514	2,615	2,739	5,281	2,640	2,113	1,910
36	996	1,480	1,007	1,478	2,213	2,465	4,324	2,694	1,940	1,887
37	639	1,612	1,114	1,200	2,385	1,857	3,486	2,036	1,694	1,652
38	459	1,015	1,048	1,061	1,982	1,990	2,263	1,736	1,356	1,356
39	340	1,359	469	793	1,103	1,271	1,358	1,024	735	775
40	292	1,210	503	577	1,419	1,077	997	701	587	417
41	240	1,021	145	482	682	729	632	491	273	264
42	183	587	323	389	568	500	297	345	175	144
43	140	518	108	207	316	206	216	172	153	69
44	37	232	108	131	136	142	129	92	82	29
45	28	77	107	64	133	66	37	117	37	32
46	0	24	36	31	51	44	68	-	97	0
47	9	9	-	22	51	26	0	-	60	7
48	-	16	-	0	25	13	7	-	0	8
49	-	0	-	19	0	-	3	-	56	-
50	-	3	-	-	49	-	-	-	-	-
Total	64,039	125,885	47,867	21,100	38,626	114,825	210,358	148,402	139,878	95,682
Mean length	26.80	27.23	28.57	33.41	33.29	24.34	25.62	27.53	25.71	26.75

AGE DATA AND GROWTH PARAMETERS

Limited age data were available for Div. 4VWX redfish from 1974 Canadian commercial samples (Parsons, personal communication).

Von Bertalanffy growth parameters (Gulland, 1969) were calculated for both males and females and are listed in Table 4 (Parsons, personal communication). The parameters are within the range reported by Sandeman (1969) for other redfish stocks within the North-west Atlantic. Age data from other areas indicate that large fish in the Div. 4VWX sample were relatively younger than would have been expected if from other areas. As a result, the validity of the upper portions of the growth curves is questionable.

Table 4. Von Bertalanffy growth parameters and parameters used in yield per recruit calculations.

Parameter	Males	Females
L_{∞} (cm)	40.662	44.737
W_{∞} (kg)	1.00	1.35
K	0.102	0.079
t_0	0.280	-1.795
t_{λ}	45.0	45.0
t_p	3.0	3.0
t_p^1	6.0-9.0	6.0-9.0
M	0.1	0.1
F	0.0-0.7	0.0-0.7

ESTIMATED TOTAL MORTALITY

An estimate of Z was made by the method of equating $-Z$ to the slope of the catch curve. The limited age data available for Div. 4VWX suggested that redfish grow about 1 cm per year in the 25 to 40 cm length range. Four catch curves over the period 1971 to 1974 were calculated using initial midpoints of 26, 29, 32, and 35 cm in 1971 to represent successive age groups. The number in each group for a particular year was estimated by taking the mean number per cm interval over a range of 3 cm and advancing the midpoint 1 cm each year. For example, the number used for the length category of 26 cm in 1971 was the mean of the observed catch numbers at 25, 26, and 27 cm. Abundance estimates for each year for each length category were calculated by dividing mean number caught by adjusted yearly effort (Table 5). Catch curves were then calculated for the four categories giving Z estimates of .36, .39, .38, and .46, respectively.

Table 5. Length abundance indices used in estimating Z.

Length category (1971)	1971	1972	1973	1974	Est. Z
26 cm	1.440	1.481	0.796	0.465	0.36
29 cm	1.108	0.968	0.282	0.053	0.39
32 cm	0.697	0.331	-0.117	-0.435	0.38
35 cm	0.517	-0.234	-0.624	-0.901	0.46

The mean of these four estimates is $Z = 0.40$.

YIELD PER RECRUIT

A yield per recruit analysis was carried out using the parameters from the von Bertalanffy growth curves. The parameters used in the yield calculations are listed in Table 4. Yield curves are shown in Fig. 1. Commercial length frequencies for 1971 through 1974 indicate that the assumption of $t_{\rho}^1 = 6$ (the age at entry to the exploited phase of the population) which corresponds to a length of approximately 20 cm is most correct. Maximum yield per recruit would occur at $F_{max} = 0.20$ for females and 0.16 for males at $t_{\rho}^1 = 6$. If $t_{\rho}^1 = 9$, F_{max} is 0.32 for females and 0.30 for males but a value of 9 years is thought to be high considering length frequency data over the period 1970 to 1974.

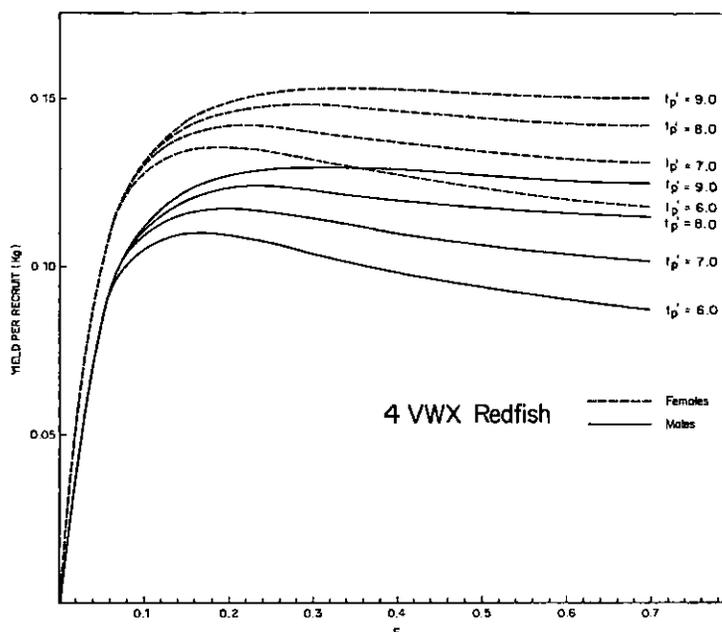


Fig. 1. Yield per recruit curves for Div. 4VWX redfish.

SURVEY DATA

Stratified-random sampling surveys (as outlined by Halliday and Kohler (1971)) have been carried out by Canada on the Scotian Shelf from 1970 to date. Biomass and population number estimates from these survey cruises are available for the period 1970 to 1974 (Table 6). These estimates suggest an increase in both biomass and numbers from 1970 through 1972 with a decline in 1973 and 1974. Estimated population length frequencies from Canadian survey cruises are listed in Table 7. Length frequencies for 1974 suggested improved recruitment compared to the four previous years.

Table 6. Div. 4VWX biomass and population number estimates from Canadian survey cruises, 1970-1974.

Div.	1970	1971	1972	1973	1974
Biomass estimate (metric tons)					
4V	53,540	71,750	27,710	29,100	37,370
4W	99,620	45,680	33,530	27,060	11,950
4X	19,180	68,830	168,010	140,360	40,270
Total	172,340	186,260	229,250	196,520	89,590
Population number estimates ($\times 10^{-6}$)					
4V	131.5	152.0	115.2	95.4	95.2
4W	481.4	152.3	122.1	94.6	48.6
4X	58.9	369.7	494.5	527.7	209.8
Total	671.8	674.0	731.8	717.7	353.6

Table 7. Div. 4VWX redbfish - estimated population length-frequencies from Canadian research vessel surveys.

Length (cm)	Number of fish x10 ⁻⁶				
	1970	1971	1972	1973	1974
<10	1.2	1.4	1.5	0.2	0.3
11	2.6	0.7	0.3	1.1	1.0
12	2.5	1.6	0.7	1.3	1.5
13	1.8	3.0	1.2	1.6	4.0
14	1.5	3.2	1.9	1.8	11.1
15	3.4	3.5	5.8	3.4	28.8
16	7.5	3.6	6.2	3.5	41.8
17	18.5	15.8	14.1	3.2	46.9
18	33.8	38.3	20.0	7.4	26.9
19	42.3	36.4	26.5	12.1	12.4
20	60.7	53.6	27.5	14.0	7.2
21	67.7	50.9	48.3	24.5	6.4
22	71.7	52.8	53.0	53.4	11.8
23	61.4	52.2	70.7	95.0	10.5
24	47.1	48.1	81.2	93.7	10.1
25	36.2	53.5	64.7	99.3	11.1
26	28.6	42.6	49.0	87.4	10.3
27	24.2	35.3	33.6	65.2	11.7
28	21.9	21.7	29.1	39.2	10.8
29	18.9	19.8	26.4	26.2	11.5
30	19.6	23.6	33.0	19.6	7.4
31	17.1	18.0	27.3	13.0	9.6
32	14.7	16.8	21.4	12.5	9.4
33	12.4	12.3	21.5	9.8	10.5
34	13.0	13.1	14.0	6.4	10.0
35	10.7	14.3	12.2	5.1	7.7
36	6.7	12.6	16.0	6.0	7.1
37	7.3	9.7	13.0	3.8	4.5
38	3.9	4.2	6.0	3.1	4.3
39	2.8	2.9	3.8	1.8	2.9
40	2.1	2.4	1.0	1.6	1.4
41	1.6	1.3	0.3	0.5	0.8
42	2.1	1.5	0.4	0.4	1.2
43	1.6	1.2	0.1	0.5	0.5
44	1.6	0.5	-	-	0.2
45	1.4	0.6	-	0.1	0.1
Totals	672.1	673.0	731.7	717.7	353.6
Mean length	24.18	24.78	25.53	25.30	22.70

MAXIMUM SUSTAINABLE YIELD

The relationship between catch and effort for the years 1942 to 1974 was examined using the generalized stock production model of Pella and Tomlinson (1969). The regression of catch per unit of effort (C/E) on effort was fitted according to the method proposed by Fox (1975).

The parameter m in the Fox equation was set equal to 2.0 to simulate the Schaefer (1954) logistic model. The model was run with 8- and 12-year average effort periods.

The C/E from 1942 to 1974 was derived from USA catches in which redbfish comprised 50% or more of the total catch in weight. Unadjusted C/E values were calculated by summing the catch and the corresponding effort from these trips using all vessel sizes.

Between 1964 and 1974 the USA redbfish fleet fishing in Div. 4VWX underwent a distinct change in vessel size composition (Table 8) shifting from a predominance of 105-215 ton vessels to 216-440 ton vessels. Also, beginning in 1968, the 441-500 ton vessels began to account for an increasing proportion of the total USA redbfish catch. As indicated by the data in Table 8, the larger vessels generally exhibited higher catch rates than smaller ones. To account for the effect of the gradual shift in size composition of the fleet

on the overall C/E index, the effort of each size category was adjusted in terms of a standard against which all other vessel categories were adjusted for each year from 1964 to 1974.

Table 8. US redfish catch (metric tons) and C/E (000 lbs) by vessel tonnage category in ICNAF Div. 4VWX.

	Tonnage category (gross tons)			
	105-215	216-310	311-440	441-500
<u>1964</u>				
C/E	32.51	46.42	51.10	-
Catch	11,368	2,411	1,636	
%	73.75	15.64	10.61	
<u>1965</u>				
C/E	41.77	67.17	74.90	-
Catch	8,886	2,898	1,182	
%	68.53	22.35	9.12	
<u>1966</u>				
C/E	47.16	82.94	74.58	-
Catch	7,808	4,860	3,982	
%	46.89	29.19	23.92	
<u>1967</u>				
C/E	43.40	64.34	48.80	-
Catch	2,775	1,658	1,882	
%	43.94	26.25	29.80	
<u>1968</u>				
C/E	48.37	71.88	88.69	82.98
Catch	1,119	919	2,349	177
%	24.52	20.14	51.47	3.88
<u>1969</u>				
C/E	63.94	52.19	86.24	75.38
Catch	551	147	313	89
%	50.09	13.36	28.45	8.09
<u>1970</u>				
C/E	40.73	36.93	92.80	80.58
Catch	406	164	362	907
%	22.08	8.92	19.68	49.32
<u>1971</u>				
C/E	59.63	53.88	99.14	81.68
Catch	2,997	601	1,277	1,334
%	48.27	9.68	20.57	21.48
<u>1972</u>				
C/E	58.19	57.13	69.62	85.29
Catch	3,502	3,076	3,559	2,189
%	28.41	24.96	28.87	17.76
<u>1973</u>				
C/E	45.29	47.53	64.13	43.61
Catch	2,157	4,178	3,636	746
%	20.13	38.98	33.93	6.96
<u>1974</u>				
C/E	37.52	49.18	50.10	61.13
Catch	681	3,944	2,456	1,774
%	7.69	44.54	27.74	20.03

In addition, the C/E index was adjusted for increases in fleet efficiency caused for example by the introduction of echo sounding gear beginning in 1952. Conversion of the entire fleet was considered to be complete by 1964. An efficiency increase of 30% in effort was assumed to have gradually taken place during the 13-year period from 1952 to 1964. The expression, e_{kt} , proposed by Halliday and Doubleday (1975) to account for changes in efficiency was used to adjust the C/E in each year from 1952 to 1974 such that

the adjusted C/E decreased by a constant percentage every year for each of the 13 years. Using a k of 0.0274 (2.74% decrease per year) resulted in an adjusted decline of 30% in effective catch per day fished after 13 years. This 30% adjustment was then applied to each succeeding year from 1965 to 1974.

Between 1942 and 1951, the Div. 4VWX redfish fishery was undergoing the initial exploitation of an accumulated stock of older individuals. The C/E during this period of expansion was not adjusted.

Total annual effort was calculated by summing the Div. 4VWX redfish catches of all countries and dividing this sum by the adjusted C/E of the USA fleet.

The resulting yield curves for 8-year and 12-year averaging periods derived from the regression of C/E on the estimated total effort are illustrated in Fig. 2. The correlation coefficients of the regressions were 0.43 and 0.44 for the 8-year and 12-year averaging periods, respectively. The slopes of both regressions, as determined by a t-test, were significant at the 95% probability level.

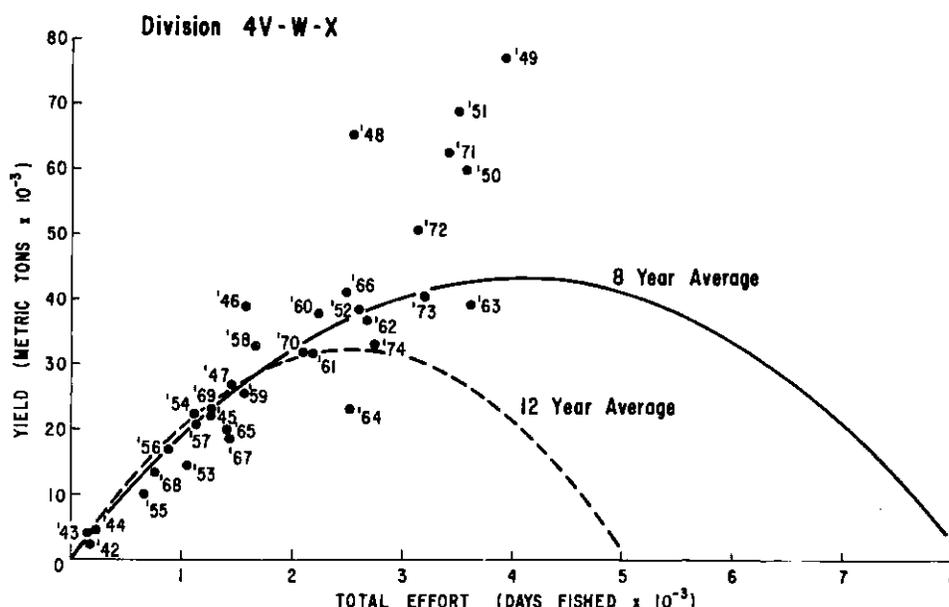


Fig. 2. Yield curves for production model for Div. 4VWX redfish.

An MSY of 43,500 tons at an effort of 4,000 tons fished was estimated using the 8-year effort average. Using a 12-year averaging period resulted in an estimated MSY of 32,300 tons at an effort of 2,500 days fished.

SUMMARY AND CONCLUSIONS

The historical catch data show that two periods of high exploitation have existed in the fishery since the early 1940's. Results from Canadian survey cruises in Div. 4VWX indicated increasing abundance in the period 1970 through 1972 followed by a decline in 1973 and 1974.

Catch curves were calculated for separate length categories over the period 1971 to 1974 giving an estimated Z of 0.4.

Yield per recruit was calculated with parameters from the von Bertalanffy growth equation with an assumed M = 0.1. If length at first capture were 20 cm corresponding to an age of six years, F_{max} would be between 0.16 and 0.20. However, if length at first capture were to be increased to 25 cm corresponding to age 9 years, F_{max} would be between 0.32 and 0.30. Commercial length frequencies for the period 1970 to 1974 suggest that an age at first capture of 6 years is a more appropriate representation of recent fishing patterns.

Estimated maximum sustainable yields using a Schaefer production model with 8-year and 12-year averaging periods are 43,500 and 32,300 tons, respectively. The corresponding effort for the two estimates are 4,000 and 2,500 days fished. Since the estimated effort at MSY for the 8-year average is greater than any observed data point, this MSY appears to be too high. The curve based on the 12-year average effort, however, appears to fit the data more reasonably. The MSY and the effort are approximately equal to catch and effort observed in 1974. Also, given the evidence presented earlier on length frequencies and growth, a 12-year average effort period is more reasonable to assume for redfish.

Thus, catches and commercial catch rates have declined in 1973 and 1974 close to average long-term levels. Research vessel survey population estimates also declined in 1973 and 1974. The general production models indicate that at least the high 1971 and 1972 catches were greater than the MSY level. Mortality in 1971-74 calculated to be $Z = 0.40$ was probably above that giving maximum yield per recruit. The total catch in 1974 of 32,819 tons was obtained with an F value approximately equal to 0.3. Given the same population size, the resulting catch at F_{max} (0.18) is 19,000 tons. Thus, continued catches at the 1974 level are unlikely to reduce mortality and may cause a decline in population size unless offset by recruitment greater than indicated for 1975.

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An Analysis of the Silver Hake Fishery on the Scotian Shelf¹

by

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ABSTRACT

Age compositions of silver hake (*Merluccius bilinearis*) taken in the USSR commercial fishery are estimated by modal analysis of monthly length frequency samples. Growth rates in the first three years of life, and size and age at maturity are examined. Canadian research vessel survey results are discussed. Virtual population analysis and catch projections are applied to USSR catches and yield per recruit calculations are carried out. The relationship between water temperature in the year of spawning and subsequent year-class success is discussed. Analysis shows that the USSR commercial catches consist mainly of age 2 fish and contain a substantial proportion of immature fish.

INTRODUCTION

The USSR is the only major exploiter of silver hake on the Scotian Shelf (ICNAF Division 4VWX). Nominal catches increased from 2 tons in 1961 to 123,000 tons in 1963, but declined to 2,500 tons by 1967 (Table 1). A second major increase in catches began in

Table 1. Nominal catches (metric tons) of silver hake from the Scotian Shelf (Div. 4VWX) by division and country.

Year	Nominal catches by division					Nominal catches by country				
	4Vn	4Vs	4W	4X	Total	Canada	Japan	USSR	USA	Others
1960	-	-	-	187	187	-	-	-	187	-
1961	-	-	-	2	2	-	-	-	2	-
1962	-	-	8,825	29	8,854	-	-	8,825	29	-
1963	168	-	116,388	6,472	123,028	-	-	123,023	5	-
1964	32	-	62,905	18,210	81,147	-	-	81,147	-	-
1965	180	2	49,461	379	50,022	5	-	49,987	27	3 ²
1966	40	-	3,860	6,423	10,323	-	-	10,323	-	-
1967	-	-	1,834	643	2,483	-	6 ¹	2,476	1	-
1968	2	237	3,150	58	3,523	5	76 ¹	3,441	1	-
1969	-	1,230	43,563	1,558	46,564	-	213 ¹	46,323	-	28 ³
1970	-	5,116	158,938	4,991	169,045	-	129	168,916	-	-
1971	11	3,000	119,452	6,190	128,653	-	8	128,633	1	11 ⁴
1972	-	75	108,769	5,204	114,048	-	63	113,774	-	211 ⁵
1973	-	3,431	265,105	30,085	298,621	-	88	298,533	-	-
1974 ⁷	90,342	10	67	89,984	-	281 ⁶

¹ Not recorded by division.

² France (St. Pierre).

³ German Democratic Republic (GDR).

⁴ Spain.

⁵ Federal Republic of Germany (10 tons) and Cuba (201 tons).

⁶ Federal Republic of Germany (FRG).

⁷ Provisional statistics (ICNAF, MS 1975).

1969 with a peak catch of 169,000 tons in 1970. Catches remained above 100,000 tons in 1971 and 1972 and increased to 299,000 tons in 1973. Catches of 90,000 tons in 1974 were limited by catch quota. A catch quota of 120,000 tons is in effect for 1975. Most of the catches have been taken in ICNAF Div. 4W.

Several assessments of the status of silver hake on the Scotian Shelf have been presented to the Assessments Subcommittee of ICNAF (Halliday, MS 1973, unpublished MS 1974; Doubleday, unpublished MS 1975). The 1973 and 1974 assessments were based on the age composition data of USSR commercial catches. It was noted in 1974 that events in the fishery, particularly the large 1973 catches, could not be adequately explained using the available data. Anderson and Nichy (MS 1975), using a new ageing technique for silver hake in Subarea 5, demonstrated that there are substantial differences in interpretation of age from otoliths between USSR and USA scientists, the age readings of USA scientists being one to two years younger. It was concluded by the authors that similar ageing problems for silver hake in Subarea 4 caused the difficulties in explaining fishery events on the Scotian Shelf. Thus, Doubleday (unpublished MS, 1975) reassessed the Subarea 4 stock using Div. 5Y silver hake age length keys obtained by the new USA technique (Dr E. Anderson, personal communication). This analysis suggested that the fishery was largely dependent on age 1 and age 2 fish and that the 1976 fishery will be heavily dependent on the strength of the 1974 year-class for which no reliable information is available.

This paper describes the growth of Subarea 4 silver hake from length-frequency data (i.e. independently from previous ageing techniques), the age composition of commercial and research vessel survey catches, and size and age at sexual maturity. From these analyses, the validity of Doubleday's previous analysis of the fishery is assessed, and inferences are made on which future management policy can be based.

DISTRIBUTION AND STOCK STRUCTURE

Canadian research vessel survey catches in July 1970-72 indicate that silver hake

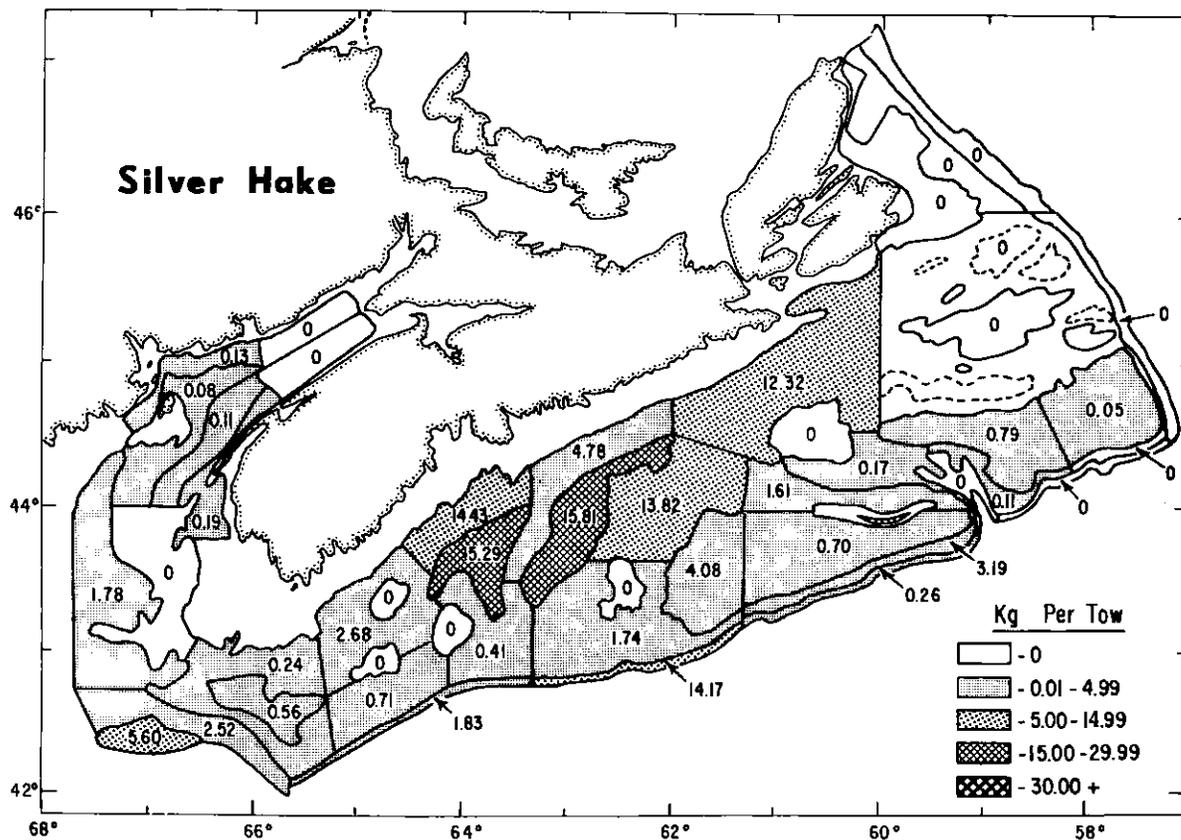


Fig. 1. Distribution and abundance of silver hake in Canadian research vessel surveys, 1970-72.

are widely distributed on the Scotian Shelf, except in the cold water area to the north of Banquereau and in the head of the Bay of Fundy (Fig. 1). Highest catch rates were in the deep holes and along the continental slope in depths greater than 100 fm in the central shelf area (the Scotian Gulf) and to the north of Sable Island Bank. A small concentration was also located in the Fundian Channel between Browns and Georges Banks. These areas of the shelf are frequently inundated with incursions of warm "slope water".

Major spawning concentrations occur on the west bar of Sable Island Bank, with spawning taking place between June and August (Sarnits and Sauskan, 1967; Halliday, personal observation). It is likely that silver hake caught in Div. 4V are taken from the eastern fringe of the Sable Island Bank stock. As the dividing line between Div. 4W and 4X runs through the centre of the Scotian Gulf which is a major area of concentration of the Sable Island stock, it is likely that much of the catches recorded from Div. 4X are also from the Sable Island stock. Concentrations of silver hake do occur and are fished in the Browns Bank area. This may be a small separate stock or part of the Georges Bank or Gulf of Maine stocks.

AGEING

Due to controversy over the ageing of silver hake by otoliths (Anderson and Nichy, MS 1975), methods of estimating mean length at age and numbers at age using only length frequency samples were examined. The fitting of parabolas by least squares to the logarithms of numbers of fish at length, a method proposed by Buchanon-Wollaston and Hogeson (1929) was found to yield good estimates of mean length at age and fair estimates of numbers at age for ages 1 and 2 and, in some cases, for age 3. A nominal date of spawning of 30 June was adopted, and the age of fish increased one year on 1 January.

Estimation of age compositions by modal analysis of length frequency samples from USSR catches of silver hake in Div. 4W was carried out using a Hewlett-Packard 9821A programmable calculator and plotter. The first step consisted on entering numbers at length and plotting the natural logarithms of numbers at length against length (Fig. 2).

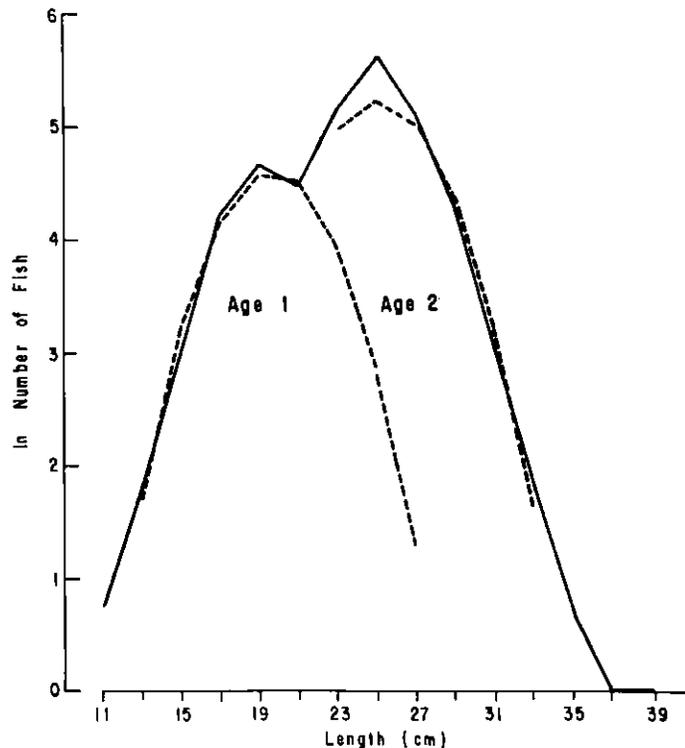


Fig. 2. Parabolas fitted to USSR length frequency samples for August 1972.

A parabola was then fitted to the lengths corresponding to the youngest age-group. Whenever possible, one length group or more to the right of the first mode was included in the

fitting procedure. When the first parabola was fitted, the remaining length frequencies were corrected to remove the estimated numbers of fish in the first age-class. The fitting procedure was repeated for the second age-group, and, when possible, for the third. In some cases, adequate separation of the modes for successive age-classes was not observed and the sample was recorded as unresolved. The parabola of logarithms of length frequencies arises from the normal probability density function. The overlap of length distributions for successive ages is the reason for beginning with the youngest and successively proceeding to older age-groups. Some judgement is required to determine where the overlap occurs.

This method of ageing was applied to the October, November and December 1973 length frequencies given in Table 1 of Anderson and Nichy (MS 1975), in order to compare the length frequency method with ageing by otoliths. Fig. 3 shows the fitted parabolas for

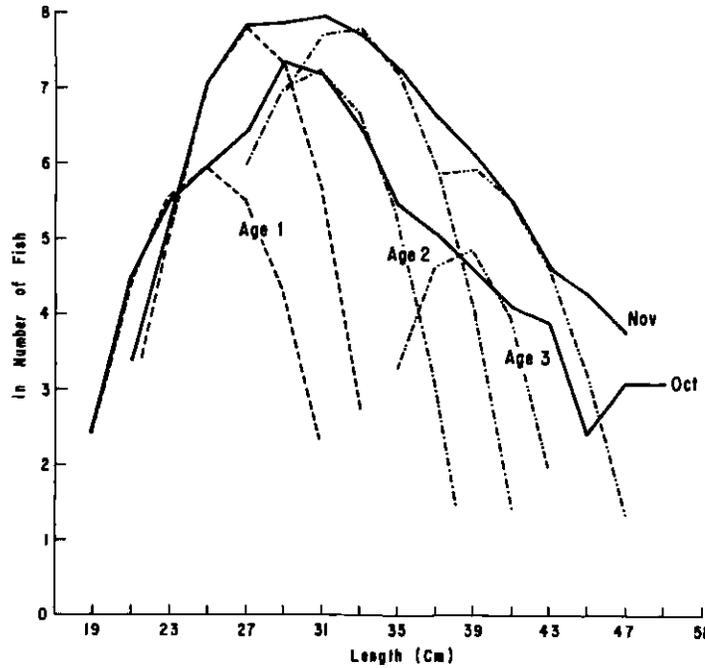


Fig. 3. Parabolas fitted to data from Table 1 of Anderson and Nichy (MS 1975).

the October and November samples; the December sample was unresolved. The methods are in agreement for ages 1 and 2 but not for age 3, as indicated from the following mean lengths (cm) at age:

Age	Length frequency method		Otolith method ¹
	Oct 1973	Nov 1973	Oct-Dec 1973
1	25.0	27.2	25.2
2	30.6	32.2	30.3
3	38.4	38.2	34.5

¹ Anderson and Nichy (MS 1975).

The analysis of Canadian research vessel length frequencies for Div. 4W silver hake indicated that recording of silver hake lengths by 1-cm groups instead of 2-cm groups is preferable, since the number of points would be doubled for the curve-fitting process.

GROWTH

Table 2 contains estimated mean lengths at age for USSR silver hake catches from ICNAF

Div. 4W from 1969 to 1974. Earlier years were not included due to fluctuations in the number of samples taken from year to year.

Table 2. Mean lengths (cm) at age by month from USSR silver hake commercial catch length frequencies, 1969-74. (Asterisks indicate samples from which age components could not be resolved.)

Age (months)	Mean length by year-class							
	1966	1967	1968	1969	1970	1971	1972	1973
6	-	-	-	-	-	12.7	-	-
9	-	-	12.8	-	-	-	14.6	*
10	-	-	-	13.9	-	16.5	*	17.3
11	-	-	-	16.3	-	18.6	18.5	18.7
12	-	-	20.3	*	-	-	18.3	19.1
13	-	-	-	19.3	-	20.7	20.7	21.5
14	-	-	-	21.4	-	21.3	22.6	22.6
15	-	-	-	22.5	21.6	21.3	23.1	25.2
16	-	-	21.1	24.0	-	22.7	24.7	25.5
17	-	-	23.6	25.8	-	24.0	24.6	*
18	-	-	-	25.5	26.5	-	-	26.0
19	-	27.0	*	-	-	-	-	-
20	-	-	-	-	-	26.7	-	-
21	-	26.9	26.2	26.8	25.7	26.0	25.6	-
22	-	-	26.9	-	27.2	*	27.1	-
23	-	29.2	27.1	-	27.7	28.1	26.2	-
24	-	29.1	*	-	*	28.5	29.1	-
25	-	29.8	28.7	-	27.5	28.4	30.0	-
26	-	-	28.2	-	*	29.2	29.8	-
27	-	-	28.7	29.8	26.7	29.3	30.7	-
28	-	*	29.3	-	29.7	29.8	31.0	-
29	-	29.0	30.2	-	*	30.0	31.4	-
30	-	-	31.1	32.1	-	-	*	-
31	32.6	-	-	-	*	-	-	-
32	33.1	*	*	30.1	-	31.2	-	-
33	-	*	*	31.3	*	31.6	-	-
34	-	31.1	-	*	*	*	-	-
35	-	*	-	33.0	*	-	-	-
36	-	*	-	*	*	*	-	-
37	-	*	-	-	*	*	-	-
38	-	*	-	-	*	*	-	-
39	-	-	-	-	*	*	-	-
40	-	-	-	-	*	-	-	-
41	-	-	-	-	-	-	-	-
42	-	39.5	-	-	-	-	-	-

Fig. 4 illustrates the monthly growth of Div. 4W silver hake based on length frequency data in ICNAF Sampling Yearbooks. It appears that growth is most rapid from March to June and September to December with a slower rate from July to September and January to March. The wavy curve was drawn free-hand to follow the seasonal trends. Attempts to fit a von Bertalanffy growth curve to these data were unsuccessful so that the following empirical procedure was adopted. From 19 months onward, the growth rate appeared to be roughly constant and the line

$$L = 17.85 + 0.428A \quad (r^2 = 0.78)$$

was fitted by least squares, where A is the age in months and L is the length in cm. Fish in a length group were assigned the mid-length of the interval (i.e., 16.00-17.99 cm became 17 cm). Growth from 9 to 21 months was estimated by fitting a quadratic curve.

$$L = -9.606 + 3.314A - 0.0762A^2 \quad (r^2 = 0.92)$$

Age-1 fish are approximately 13 cm long in March and reach 26 cm by December. By the following December, they are 31 cm long.

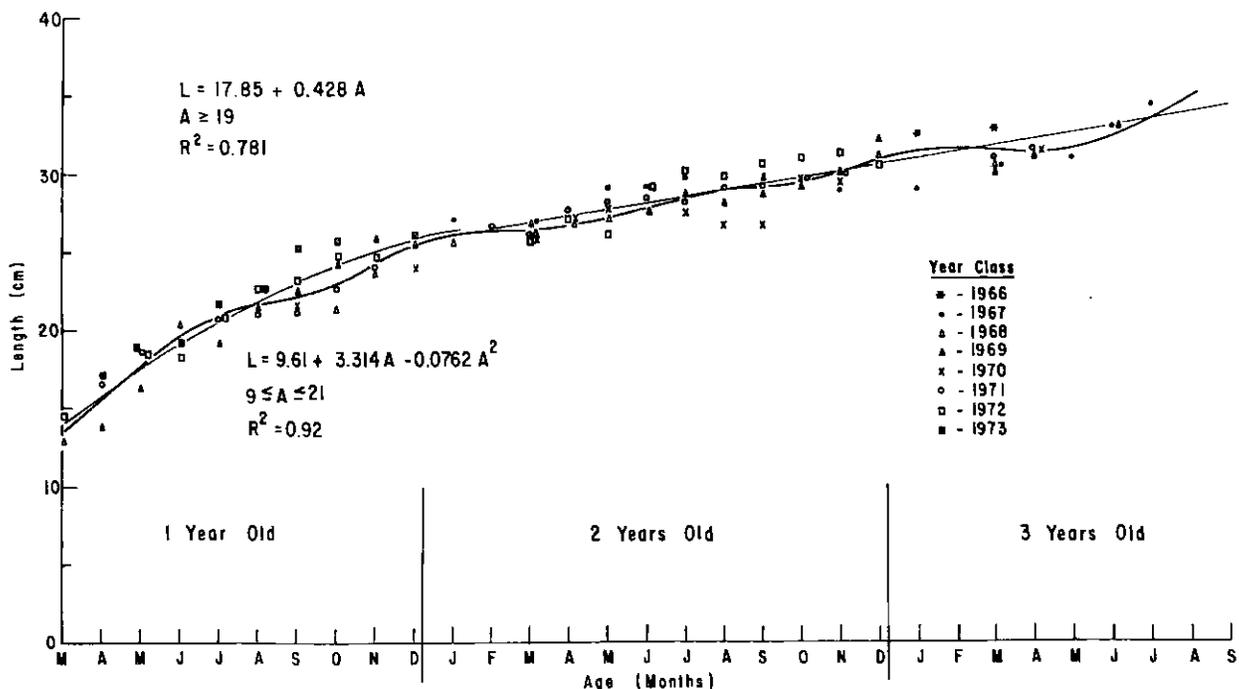


Fig. 4. Estimated length at age for silver hake in Div. 4W based on USSR length frequency samples.

CANADIAN RESEARCH VESSEL CATCHES

Canada has conducted groundfish inventory cruises by research vessel, covering the entire Scotian Shelf, in the late June to early August period of each year from 1970 (Halliday and Kohler, MS 1971). Silver hake has a low availability to the gear used (probably due to the low headrope height of approximately 9 ft (2.7 m)) and uncorrected estimates of population biomass are substantially below recent catch levels (Table 3). Surveys suggest that abundance declined in 1971 from the 1970 level, increased in 1972 and again in 1973 to above the 1970 level, and then decreased slightly in 1974.

Table 3. Silver hake in Div. 4VWX: estimates of biomass, population numbers and catch per tow from Canadian research vessel surveys, 1970-74.

Year	Biomass (tons)	Catch/tow (kg)	Population numbers (millions)	Catch/tow (numbers)
1970	23,520	4.90	142.7	29.32
1971	7,880	1.59	53.3	10.78
1972	15,260	3.09	87.9	17.72
1973	38,190	7.69	229.9	46.29
1974	36,140	7.28	183.5	36.95

Survey estimates of population length-frequencies contain a wider range of sizes than those of commercial catches and are distinctly bimodal with modes at approximately 20 cm and 28 cm (Table 4). The above growth analysis from commercial catch length frequencies confirm that these modes represent 1-year-old and 2-year-old fish respectively. Analysis of survey length frequencies shows that most of the catch consists of age-2 fish (Table 5)

Sex ratios in survey catches in Div. 4W are fairly consistent for age-2 fish, approximately half as many males as females being caught (Table 6). At age 1, however, the ratio of males to females has declined from 1.6 in 1971 to 0.5 in 1974.

Table 4. Silver hake in Div. 4VWX: estimated length composition of population from Canadian research vessel surveys, 1970-74.

Length (cm)	Population numbers ($\times 10^{-3}$)				
	1970	1971	1972	1973	1974
≤10	37	90	-	-	-
11	-	-	46	47	71
12	68	46	-	48	-
13	34	123	139	313	17
14	239	534	371	672	187
15	645	1,139	1,128	1,346	384
16	1,297	1,649	1,467	2,149	552
17	2,111	2,620	2,689	4,274	1,680
18	3,790	5,797	3,066	8,355	3,864
19	4,554	4,318	3,921	12,767	6,146
20	6,490	2,520	3,986	13,554	8,854
21	7,991	1,917	3,099	12,740	6,622
22	5,352	698	4,650	9,886	5,174
23	2,938	512	3,462	4,432	2,478
24	1,342	241	1,527	2,377	1,824
25	3,317	728	3,762	3,015	3,203
26	9,987	1,237	7,423	9,940	10,048
27	18,389	3,946	11,402	22,291	20,435
28	24,417	6,255	11,135	36,325	25,129
29	19,768	5,635	6,245	30,186	20,849
30	10,210	3,883	4,474	19,849	18,736
31	6,765	2,603	2,118	10,221	11,930
32	3,375	1,999	2,705	4,486	7,307
33	2,197	1,489	1,768	3,506	7,197
34	1,711	805	1,524	2,283	4,320
35	885	337	1,391	2,615	2,735
36	838	306	1,153	2,271	2,442
37	953	349	557	1,986	2,200
38	203	77	360	1,201	1,265
39	550	114	218	975	600
40	376	99	170	529	561
41	252	87	280	801	624
42	100	71	188	547	781
43	394	203	114	730	440
44	174	248	65	209	670
45	120	145	87	426	366
46	138	-	-	322	413
47	240	157	142	479	877
48	140	104	50	270	355
49	136	55	101	34	410
≥50	158	158	848	1,419	1,797
Total	142,681	53,294	87,831	229,876	183,543

Table 5. Silver hake in Div. 4VWX: estimated age composition of the population from Canadian research vessel surveys, 1970-74.

Age	Population numbers ($\times 10^{-6}$)				
	1970	1971	1972	1973	1974
1	38.3	21.3	31.9	70.8	36.4
2	100.8	26.1	46.9	148.5	120.0
3+	3.6	5.9	9.0	10.6	27.1
Total	142.7	53.3	87.8	229.9	183.5

Table 6. Silver hake in Div. 4VWX: sex ratios for ages 1 and 2 from Canadian research vessel surveys, 1971-74.

Age	Sex ratios (male : female)			
	1971	1972	1973	1974
1	1.62	1.52	0.93	0.50
2	0.48	0.43	0.29	0.68

SIZE AND AGE AT SEXUAL MATURITY

Observations on sexual maturity of silver hake were made on research vessel cruises and the basic data for 1971 to 1974 are given in Table 7. On the average, over the four years, almost all males greater than 25 cm in length were mature, the 50% maturity point

Table 7. Silver hake in Div. 4VWX: size distribution of immature (Imm) and mature (Mat) fish by sex in Canadian research vessel surveys, 1971-74.

Sex	Length (cm)	1971		1972		1973		1974		1971-74		% Mature
		Imm	Mat	Imm	Mat	Imm	Mat	Imm	Mat	Imm	Mat	
Male	15	12	-	8	-	7	-	2	-	29	-	-
	16	11	-	11	-	5	-	5	-	32	-	-
	17	22	-	18	1	12	-	14	-	66	1	1
	18	48	-	26	-	17	-	22	-	113	-	-
	19	35	-	26	-	18	-	28	1	107	1	1
	20	24	-	31	-	21	1	30	3	106	4	4
	21	14	-	18	3	8	-	21	-	61	3	5
	22	5	-	8	5	14	-	15	4	42	9	18
	23	2	2	10	2	9	-	6	3	27	7	21
	24	-	4	6	2	4	3	6	12	16	21	57
	25	-	9	4	11	2	19	2	24	8	63	89
	26	-	14	1	22	-	52	1	43	2	131	98
	27	2	26	1	28	-	49	4	97	7	200	97
	28	-	34	-	24	-	71	-	89	-	218	100
	29	1	25	-	11	1	39	-	86	2	161	99
	30	-	14	-	16	1	24	-	82	1	136	99
	31	-	6	-	13	1	19	1	57	2	95	98
	32	-	4	-	8	-	14	-	25	-	51	100
	33	-	3	-	6	-	16	-	13	-	38	100
	34	-	-	-	2	-	8	-	3	-	13	100
35	-	-	-	-	-	3	-	2	-	5	100	
36	-	-	-	2	-	1	-	2	-	5	100	
37	-	1	-	1	-	-	-	1	-	3	100	
38	-	-	-	1	-	-	-	-	-	1	100	
39	-	-	-	1	-	-	-	-	-	1	100	
40	-	-	-	-	-	-	-	1	-	1	100	
Female	15	8	-	5	-	5	-	5	-	23	-	-
	16	12	-	6	-	4	-	8	-	30	-	-
	17	16	-	15	-	19	-	14	-	64	-	-
	18	32	2	18	-	25	-	33	-	108	2	2
	19	28	1	26	1	21	1	42	-	117	3	3
	20	19	-	38	-	16	-	48	1	121	1	1
	21	16	-	15	-	12	-	33	1	76	1	1
	22	9	-	20	2	9	1	26	1	64	4	6
	23	5	-	17	-	8	-	21	-	51	-	-
	24	1	-	11	-	6	-	20	1	38	1	3
	25	3	1	5	2	8	-	18	3	34	6	15
	26	4	4	14	3	5	16	27	6	50	29	37
	27	6	21	19	11	16	49	33	26	74	107	59
	28	9	42	16	27	17	72	29	37	71	178	71
	29	-	52	10	20	11	90	21	45	42	207	83
	30	2	54	9	21	2	81	5	69	18	225	93
	31	1	43	1	16	1	43	4	109	7	211	97
	32	1	38	4	24	2	36	1	81	8	179	96
	33	-	30	2	27	-	25	3	92	5	174	97
	34	-	24	1	26	-	11	-	67	1	128	99
35	-	9	-	19	-	24	-	43	-	95	100	
36	-	7	1	10	-	26	-	41	1	84	99	
37	-	7	-	6	-	21	-	33	-	67	100	
38	-	2	-	6	-	18	-	20	-	46	100	
39	-	3	-	6	-	17	-	8	-	34	100	
40	-	1	-	3	-	11	-	12	-	27	100	

lying between 23 cm and 24 cm. Almost all females greater than 30 cm were mature, the 50% maturity point lying between 26 cm and 27 cm. There was some variation among years.

Research vessel estimated population length frequencies from Div. 4W were taken as representative of the size composition of the actual population. Age-groups 1 and 2 were

Table 8. Silver hake in Div. 4VWX: length frequencies of ages 1 and 2 fish by sex ($\times 10^{-3}$) and percentage mature at age from Canadian research vessel surveys, 1971-74.

Sex	Length (cm)	1971		1972		1973		1974	
		Age 1	Age 2						
Male	10	-	-	4	-	-	-	-	-
	11	-	-	10	-	-	-	-	-
	12	1	-	29	-	-	-	-	-
	13	5	-	70	-	-	-	-	-
	14	20	-	155	-	-	-	3	-
	15	60	-	303	-	9	-	17	-
	16	145	-	532	-	59	-	86	-
	17	283	-	835	-	274	-	307	-
	18	444	-	1170	-	884	-	769	-
	19	561	-	1466	-	1974	-	1374	-
	20	570	-	1643	-	3042	-	1750	-
	21	466	-	1645	-	3239	-	1588	-
	22	307	-	1472	-	2382	-	1026	-
	23	163	-	1178	7	1211	2	473	4
	24	69	5	842	133	425	40	155	78
	25	24	68	538	1043	103	316	36	653
	26	7	387	308	3385	17	1232	6	3186
	27	1	1049	157	4531	2	2314	1	7816
	28	-	1352	72	2502	-	2096	-	9632
	29	-	829	29	570	-	915	-	5965
30	-	242	11	54	-	193	-	1856	
31	-	33	3	2	-	20	-	290	
32	-	2	1	-	-	1	-	23	
33	-	-	-	-	-	-	-	1	
% Mature		5.8	97.3	12.3	100.0	2.9	99.5	8.5	98.7
Female	10	-	-	-	-	-	-	-	-
	11	-	-	1	-	-	-	-	-
	12	-	-	4	-	-	-	-	-
	13	1	-	18	-	-	-	-	-
	14	4	-	58	-	-	-	7	-
	15	17	-	156	-	71	-	7	-
	16	57	-	352	-	246	-	53	-
	17	141	-	658	-	661	-	261	-
	18	263	-	1022	-	1383	-	885	-
	19	372	-	1318	-	2255	-	2070	-
	20	400	-	1411	-	2864	-	3333	-
	21	325	-	1254	-	2834	-	3697	-
	22	201	-	925	6	2184	-	2826	-
	23	94	-	567	58	1311	-	1488	16
	24	33	1	288	348	613	2	534	113
	25	9	9	122	1391	224	37	135	557
	26	2	81	43	3654	63	403	23	1921
	27	-	422	12	6323	14	2193	3	4703
	28	-	1281	3	7204	2	5950	-	8164
	29	-	2258	1	5405	-	8046	-	10060
30	-	2313	-	2670	-	5423	-	8791	
31	-	1376	-	869	-	1822	-	5448	
32	-	476	-	186	-	305	-	2395	
33	-	96	-	26	-	25	-	747	
34	-	12	-	2	-	1	-	166	
35	-	1	-	-	-	-	-	26	
36	-	-	-	-	-	-	-	3	
% Mature		1.7	94.0	1.6	51.5	2.2	88.5	1.9	71.1

separated out for males and females separately. The maturity keys in Table 7 were then applied to the length frequencies of these age-groups to obtain the proportion mature at age (Table 8). The actual ages of individual fish on which maturity observations were made are not known. Thus, the convention was used that, at length groups where age-1 and age-2 fish occur, immature fish were assigned to age 1 with the residual, if any, being assigned to age 2. This makes the reasonable assumption that younger fish of the same size are less likely to be mature.

In the years 1971-74, a very small proportion of age-1 males were recorded as mature and almost all age-2 males were mature (Table 8). Given that there will have been a small proportion of errors in assigning maturity stages and a small error in age designation, it is concluded that essentially all age-1 males are immature and all age-2 males mature.

For females, in those years, a small proportion of age-1 fish are also recorded as mature (Table 8). For the reasons cited above, it is concluded that essentially all age-1 females are immature. Substantially higher proportions of age-2 females are recorded as immature in contrast to the observations for males. As few as 6% are recorded as immature in 1971, and as many as 48% in 1972, averaging 25% for the four years. An explanation of this variation is not obvious at this time. The 1972 data, in particular, have been examined in detail for potential sources of error, but this did not provide a plausible explanation of the high proportion of immatures in that year. Thus, it is tentatively concluded that, on the average, 75% of females mature at age 2, but that this may vary from 50% to almost 100%.

LENGTH-WEIGHT KEYS

Table 9 contains parameter estimates for length-weight keys for silver hake caught in Div. 4W on Canadian research vessel cruises in July, 1969 to 1974. The relation:

$$\log_{10} W = \log_{10} A + B(\log_{10} L)$$

where the weight (W) is measured in grams and length (L) in cm. For the purpose of yield calculations, parameter estimates for all six years were averaged to give the combined key

$$\log_{10} W = -2.403534 + 3.177198 \log_{10} L.$$

Table 9. Parameters of the length-weight relationships¹ for silver hake in Div. 4W in July from Canadian research vessel surveys, 1969-74.

Year	Log ₁₀ A	B
1969	-2.296819	3.093991
1970	-2.704820	3.382850
1971	-2.264429	3.099391
1972	-2.411192	3.180211
1973	-2.343713	3.135717
1974	-2.400230	3.171025
Average	-2.403534	3.177198

¹ Equation: $W = A \cdot L^B$, where W is given in g and L in cm.

AGE COMPOSITION OF COMMERCIAL CATCHES

Ageing of USSR commercial length frequencies of silver hake in Div. 4W, using modal analysis, provides estimates of the proportion at age in the catch in the monthly samples. As noted earlier, most of the commercial catch is taken by the USSR in Div. 4W. Thus, USSR age compositions in Div. 4W are taken as representative of the entire fishery. For months for which sampling data were available, the mean weights provided with USSR samples were divided into total Div. 4W catches for that month, giving estimates of numbers removed, which were then prorated over ages.

Catches, for which there were no sampling data, were prorated on an annual basis on the annual proportions at age obtained by summing over months for which sampling data were available. Silver hake catches prior to 1965 were not broken down by month in ICNAF Statistical Bulletins. Thus, estimates of numbers removed at age could be calculated only from 1965 to 1974.

Age-1 and age-2 fish could be separated out in most catches, but it was necessary to combine fish of age 3 and older, as these age-groups could not be separated sufficiently often to provide adequate estimates of their contribution to catches.

Age-2 fish predominated in the catches of all years except 1966, and, from 1970 onwards, age-1 fish made a significant contribution in terms of numbers (Table 10). Comparison of age compositions obtained from the length-frequency analysis with those obtained from Anderson's (MS 1975) age-length keys from Div. 5Y (Table 11) and also with those obtained from USSR ageing (Table 12) indicates broad agreement on age compositions from the length-frequency analysis and the USA age-length keys, but these are substantially different from the USSR age compositions. This is supporting evidence for the general accuracy of USA ageing in Subarea 5 and casts some doubt on USSR ageing for Scotian Shelf silver hake.

Table 10. Age composition of commercial catches of silver hake in Div. 4W, 1965-74, from length-frequency analysis.

Year	Numbers at age ($\times 10^{-3}$)			Total
	1	2	3+	
1965	1,671	170,422	43,888	215,981
1966	10,220	9,795	462	20,477
1967	-	7,576	915	8,491
1968	84	18,218	2,173	20,475
1969	21,456	242,169	22,436	286,061
1970	208,319	702,322	77,926	988,567
1971	65,461	553,957	223,647	843,064
1972	149,692	414,279	120,802	684,773
1973	102,212	1,449,980	136,718	1,688,911
1974	80,432	405,044	57,153	542,629

Table 11. Age composition of commercial catches of silver hake in Div. 4W, 1968-74, from the application of Div. 5Y age-length keys (Anderson, MS 1975).

Year	Numbers at age ($\times 10^{-3}$)						Total
	1	2	3	4	5	6	
1968	11,288	8,737	2,432	203	55	77	22,792
1969	104,245	134,717	44,714	4,939	1,680	184	290,479
1970	320,628	522,578	156,226	14,123	4,563	2,369	1,020,487
1971	181,418	510,203	168,553	12,234	3,183	2,537	878,128
1972	300,142	306,441	131,866	17,004	6,589	-	762,042
1973	432,907	1,078,980	316,463	33,806	12,208	2,817	1,878,120
1974	87,830	331,433	115,173	11,876	4,971	1,105	552,388

YIELD PER RECRUIT

The growth equations and the length-weight keys indicated above were used to derive a yield-per-recruit isopleth diagram (Fig. 5). Monthly growth and mortality were calculated and yield was accumulated to 72 months of age. Yield-per-recruit calculations were based on knife-edge selection at a given age and are calculated per 9-month-old fish, i.e., $t_p = 9$ months. Nine months of age was chosen as a reference point due to the large effect

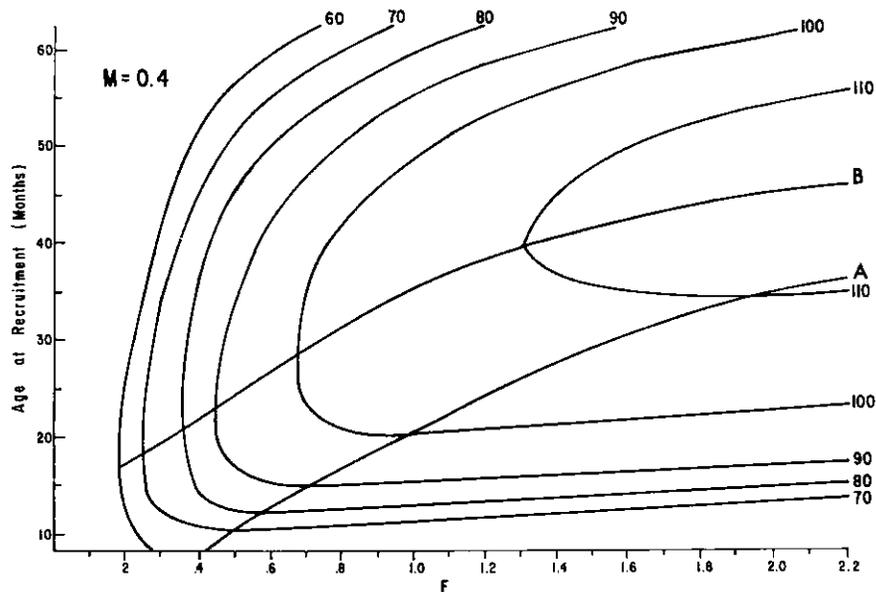


Fig. 5. Yield per recruit isopleth diagram. The lower line (A) imposed on the isopleth gives the F with greatest yield for given ages at recruitment and the upper line (B) gives the age at recruitment with greatest yield for given levels of F.

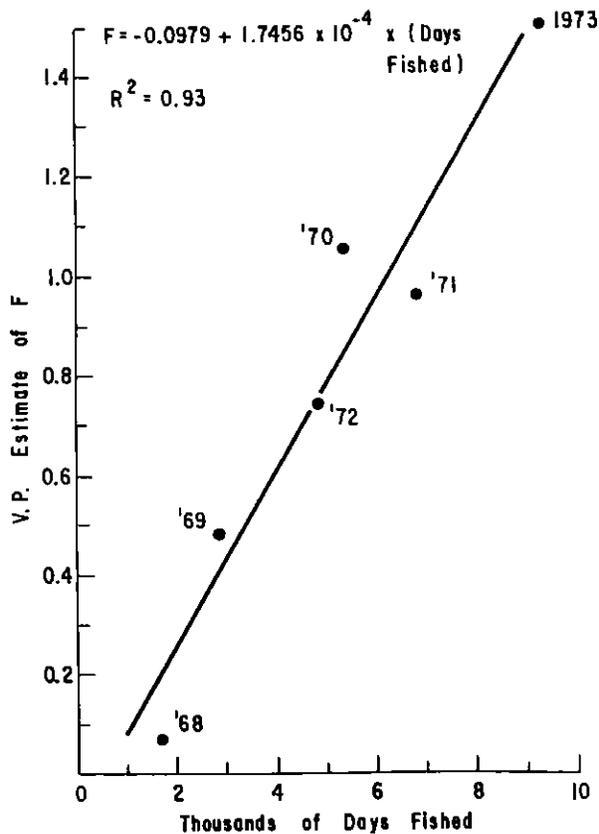


Fig. 6. Regression of virtual population estimates of F on days fished by USSR (>1800 GRT) otter trawlers.

of natural mortality (M) on year-class size, as the age of recruitment varies. A value of $M = 0.4$, similar to Anderson (MS 1975), was assumed. Identical calculations with $M = 0.5$ and $M = 0.6$ were carried out with lower yields per recruit but with qualitatively similar results with respect to the effect of fishing mortality.

Yield per recruit increases rapidly over a wide range of fishing mortalities as the age of selection increases from 12 to 18 months. Recalling that silver hake nominally reach 12 months of age in June, this observation implies that age-1 fish should not be caught at all. The current mean age of selection is approximately 15 months in the USSR silver hake fishery in Div. 4W.

Yield per recruit rises steeply as the rate of fishing mortality (F) rises to 0.5 and more slowly as F increases to 0.7. For F greater than 0.7, little increase in yield is observed. With knife-edge selection at 15 months, 0.7 is the value of F which maximizes yield per recruit (Fig. 6).

VIRTUAL POPULATION ANALYSIS AND CATCH PROJECTIONS

The numbers removed from the stock at age are probably most accurately estimated for ages 1 and 2 by length-frequency analysis, but inability to separate ages 3 and older precludes the use of virtual population analysis on these data. Although there are undesirably large differences in numbers at age between these and estimates obtained using Div. 5Y age-length keys, there are broad similarities between the two data sets. The latter are used for virtual population analysis, as they appear to be sufficiently accurate to allow meaningful examination of the relative importance of recruitment assumptions to projected catch levels for 1976.

Using $M = 0.40$, the data in Table 11 were analysed, assuming for 1974 that $F = 0.50$ for ages 2-6 and $F = 0.12$ for age 1. The F at age 6, in earlier years, was chosen to correspond to F levels for younger age-groups in the same year. Results of the calculations are displayed in Tables 13 and 14.

Means of the F-values calculated for ages 2-5 in each year fluctuate in close relationship to fluctuations in annual effort (days fished) on the Scotian Shelf by USSR otter trawlers greater than 1800 gross registered tons. The data series are as follows:

	1968	1969	1970	1971	1972	1973
Mean F (ages 2-5)	0.07	0.48	1.05	0.96	0.74	1.51
Fishing effort	1,677	2,871	5,405	6,823	4,813	9,333

These data have a correlation coefficient of $r = 0.97$ ($r^2 = 0.93$). Similar calculations, using the data of Table 12 and averaging the F-values calculated for ages 3-8, produced a correlation coefficient of $r = 0.89$ ($r^2 = 0.80$), suggesting that the data of Table 11 are more reliable than those of Table 12. The slope and intercept of the relation

Table 12. Age composition of silver hake catches in Div. 4W, 1963-74, from Rikhter (unpublished data 1975).

Year	Numbers at age ($\times 10^{-3}$)								Total
	1	2	3	4	5	6	7	8+	
1963	-	26,316	143,111	134,308	33,314	3,743	750	1,834	343,376
1964	831	6,745	92,038	131,754	26,460	6,378	486	-	264,692
1965	-	523	44,712	103,797	29,846	4,387	364	-	183,629
1966	22	3,786	4,599	6,805	3,950	565	18	-	19,745
1967	-	68	1,511	5,077	1,570	239	24	-	8,489
1968	467	6,298	11,336	1,752	583	145	276	84	20,941
1969	19,314	16,022	78,858	97,177	32,147	10,875	2,420	1,196	258,009
1970	86,630	131,550	343,014	183,496	58,867	4,236	2,672	1,279	811,744
1971	18,969	80,260	422,419	379,144	92,960	13,196	5,429	8,192	1,020,569
1972	40,953	130,957	249,592	145,966	96,815	13,929	2,651	2,413	683,276
1973	52,221	85,912	675,502	599,698	203,829	47,167	13,476	5,053	1,684,542
1974	30,145	98,317	246,892	149,370	32,782	7,490	3,233	2,649	571,378

Table 13. Estimated population numbers at age for silver hake in Div. 4W, 1968-74.

Year	Population numbers at age ($\times 10^{-6}$)					
	1	2	3	4	5	6
1968	768.2	144.0	38.3	10.6	0.7	0.4
1969	1,630.6	506.2	89.5	23.7	7.0	0.4
1970	1,832.4	1,008.6	231.2	24.7	11.9	3.3
1971	1,687.7	969.6	263.9	33.8	5.5	4.3
1972	3,017.8	984.4	247.7	45.6	12.9	-
1973	2,019.8	1,779.7	414.5	62.2	17.0	3.5
1974	975.0	1,005.3	349.3	36.0	15.1	2.0

Table 14. Fishing mortality (F) estimates for silver hake in Div. 4W, 1968-74.

Year	Fishing mortality by age-group						Mean F Ages 2-5
	1	2	3	4	5	6	
1968	0.02	0.08	0.08	0.02	0.10	0.10	0.07
1969	0.08	0.38	0.89	0.29	0.34	0.30	0.48
1970	0.24	0.94	1.52	1.11	0.61	1.00	1.05
1971	0.14	0.96	1.36	0.56	0.56	0.56	0.96 ¹
1972	0.13	0.47	0.98	0.59	0.92	-	0.74
1973	0.30	1.23	2.04	1.02	1.75	1.75	1.51
1974	0.12	0.50	0.50	0.50	0.50	0.50	-

¹ Excludes F for age 5 as this is a starting value in the calculations.

between effort and mean F was found to be insensitive to changes in M and the assumed values of F for 1975.

Estimates of numbers at age 1 from virtual population analysis indicate that recruitment improved in 1969 with entry of the 1968 year-class to the fishery, and it appears that the 1967 year-class was a modest improvement over that of 1966 (Table 13). The 1969 year-class and 1970 year-class were of comparable size to that of 1968, but the 1971 year-class was almost twice as large and the 1972 year-class was also good. The estimated size of the 1973 year-class is a direct function of the F of 0.12 chosen for 1974. The ratio of F-values for age 1 and age 2 in the previous six years varies from 0.15 to 0.28, averaging 0.23. Using the average ratio of 0.23 (i.e. that $F(\text{age } 1) = 0.115$) gives an estimate for the 1973 year-class of 975×10^6 fish. Thus, it is likely that the 1973 year-class is poorer than those of the preceding five years.

The 1974 population estimates in Table 13 are taken as the starting point for projection of potential yield in 1976 (Table 15). The calculated 1974 catch weight is 7.8% above the actual reported catch, indicating that the mean weights used are slightly high. Thus, calculated catches for 1975 and 1976 have been corrected downwards. The 1974 year-class is assumed to contain 1.0×10^9 fish at age 1. Assumptions on the strength of the 1975 year-class have an insignificant effect on 1976 catch predictions.

An $F = 0.70$ on fish of age 2+ is required in 1975 to approximately attain the quota of 120,000 tons. At the present age at recruitment of about 15 months, this value of F maximizes yield per recruit. $F_{\text{max}} = 0.70$ is applied in 1976 giving a calculated yield of approximately 100,000 tons.

This calculation is critically dependent on the F-values assumed for 1974 and the assumed size of the 1974 year-class. The assumed $F = 0.50$ for 1974 is only one-third the level of F calculated for 1973 and implies a reduction in effort to about the 1969 level of approximately 3,000 days fished. No information on 1974 effort is available at this

Table 15. Population numbers and catch predictions for silver hake in Div. 4W, 1974-76.

Age	1974			1975			1976			Mean weight (kg)	
	Stock size (10 ⁻⁶)	F	Catch weight (000 tons)	Stock size (10 ⁻⁶)	F	Catch weight (000 tons)	Stock size (10 ⁻⁶)	F	Catch weight (000 tons)		
1	975	0.115	4	1000	0.14	5	1000	0.14	5	0.051	
2	1005	0.500	53	582	0.70	39	583	0.70	39	0.159	
3	349	0.500	31	409	0.70	47	194	0.70	22	0.270	
4	36	0.500	5	142	0.70	26	136	0.70	25	0.426	
5	15	0.500	3	15	0.70	4	47	0.70	13	0.635	
6	2	0.500	1	6	0.70	2	5	0.70	2	0.905	
Calculated catch			(97)				(123)				(106)
Corrected catch ¹			90				114				98

¹ Catch weights in 1975 and 1976 adjusted by the ratio of calculated to actual catches in 1974 to correct for errors in mean weights used.

time. It seems likely, however, that the authors have erred on the conservative side. The size of the 1973 year-class is particularly sensitive to assumptions on F.

The assumed size of the 1974 year-class appears modest in comparison with the good year-classes of 1968 to 1972. However, if the comparison is extended to include 1962 to 1972, this estimate is certainly above the overall average. It must be pointed out that the 1971 and 1972 year-classes, which formed the basis of the record 1973 catch, were exceptionally strong and not an indication of what is to be expected in general. If the 1974 year-class is 50% larger than has been assumed, the projected 1976 catch is increased by 20,000 tons.

TEMPERATURE AND ABUNDANCE

The relationship between bottom temperature on Sable Island Bank in July and year-class success was examined. Bottom temperatures for the area (less than 50 fm) were obtained by averaging bottom temperature measurements taken on Canadian research vessel cruises. The number of observations used varied from 10 to 59 with about 15 for most years. Catch per hour fished of age-1 and age-2 silver hake in Div. 4W by USSR otter trawlers (>1800 GRT) was calculated using estimated numbers at age from Table 10 (Table 16). The effort data for 1974 are not yet known. Catch per unit effort of 2-year-old

Table 16. Bottom temperature on Sable Island Bank in July and catch-per-unit effort of ages 1 and 2 silver hake in Div. 4W.

Year	Temp (°C)	Catch per hour (10 ⁻³)	
		Age 1	Age 2
1965	7.56	0.04	4.40
1966	3.76	0.38	0.37
1967	5.39	0.00	5.17
1968	-	0.00	0.89
1969	4.82	0.64	7.23
1970	5.10	2.69	9.06
1971	5.92	0.71	5.97
1972	4.72	2.37	6.55
1973	4.33	0.98	13.92
1974	5.88		

fish appears to be a more reliable measure of year-class size than the corresponding data for 1-year-olds (Fig. 8). Fig. 7 shows the relation between temperature at spawning and

catch per hour fished of 2-year-olds. Evidently, temperatures near 6°C are favourable while temperatures near 4°C are unfavourable. A two-variable equation with catch per unit effort of parents and temperature in July would predict the catch per unit effort of the 2-year-old filial populations well for all year-classes except 1971. However, in view of the small number of data points, the fitting of a response surface does not appear justified.

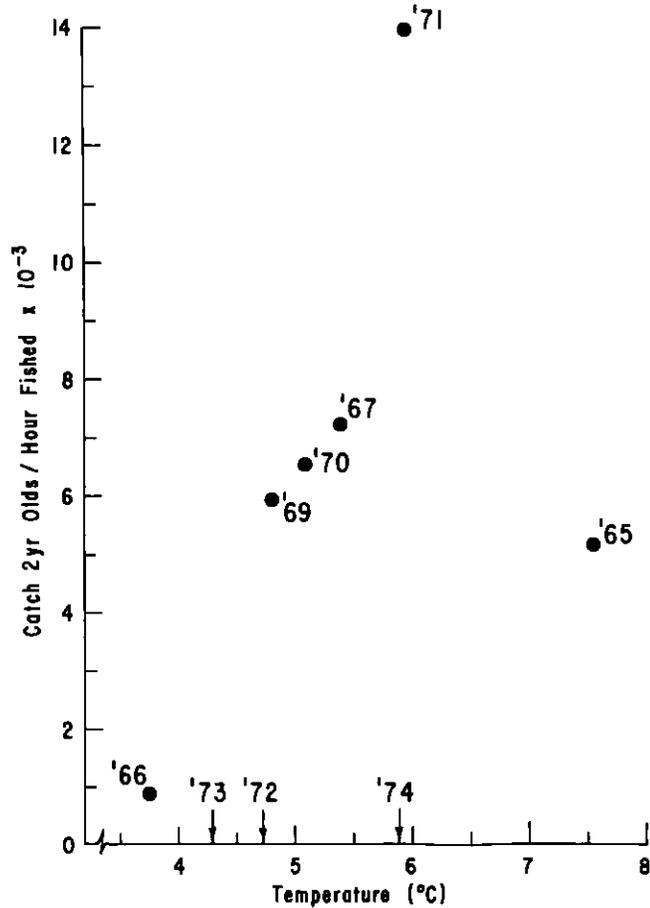


Fig. 7. Catch per unit effort of 2-year-old silver hake in relation to bottom temperature on Sable Island Bank in July of the year of spawning.

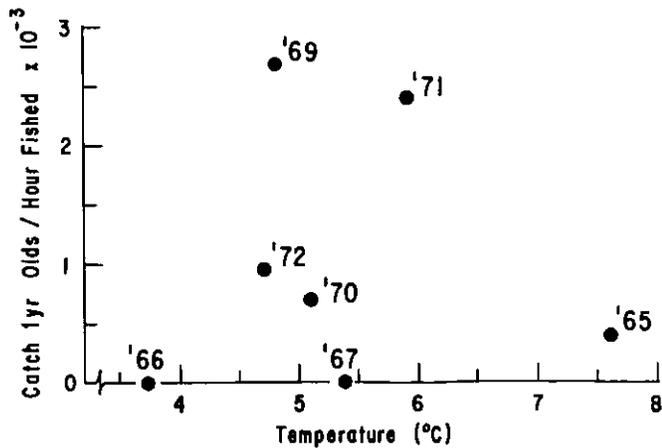


Fig. 8. Catch per unit effort of 1-year-old silver hake in relation to bottom temperature on Sable Island Bank in July of the year of spawning.

On the basis of observed temperatures for 1972-1974, the 1972 year-class is expected to be moderate, the 1973 year-class weak, and the 1974 year-class strong.

DISCUSSION

Estimation of the age composition of USSR silver hake catches in Div. 4W by analysis of length frequency samples reveals a consistent pattern of monthly growth in agreement with the results of Anderson and Nichy (MS 1975) and at variance with USSR estimates of catch at age.

Biological samples from Canadian research vessel catches indicate that a negligible proportion of 1-year-old silver hake are sexually mature. While almost all 2-year-old males are mature, the proportion of immature 2-year-old females averages 25% and can be considerably higher.

Yield-per-recruit calculations show that, for a range of natural mortality rates, yield is increased by not catching 1-year-old fish. When $M = 0.4$ and the mean age of selection is at the current level of 15 months, the optimal value for F is 0.7. Very little yield is lost by increasing the mean age of selection beyond the optimal level.

Estimated age compositions of the USSR commercial catch of silver hake in Div. 4W, derived by analysis of length frequency samples, are in agreement with age compositions derived using US age-length keys for Subarea 5. The largest proportion of the catch (in numbers) is made up of 2-year-old fish. A further large fraction consists of 1-year-old fish. Thus, a high fishing mortality is exerted on a year-class before it reaches maturity.

The current mean age of selection of 15 months has two serious implications for the future of the fishery. In terms of weight contributed to the total catch, 2- and 3-year-old fish overshadow all other ages. Thus, a sequence of two mediocre year-classes can cripple the fishery. Secondly, the breeding stock consists mainly of 2- and 3-year-old fish, so that the spawning stock biomass is extremely vulnerable to fluctuations in recruitment. There is some evidence that the 1973 year-class is poor. Increasing the mean age of selection would help to stabilize the catch and the spawning stock size by allowing greater survival to age 4.

There is some indication that year-class success and temperature are related. Available evidence suggests that the 1973 year-class is poor to moderate while the 1974 year-class is moderate to good. The availability of 1-year-old fish is variable from year to year so that the catch per hour fished of 1-year-olds shows no clear relationship with temperatures (Fig. 8).

Catch projections based on the assumption that 1974 effort was at the 1969 level and that the 1974 year-class was moderate (10^9 fish) indicate that a 1976 quota of 100,000 tons is appropriate. The assumed year-class size for 1974, while lower than those of 1971 and 1972, is high in comparison with year-class sizes over the history of the fishery from 1963 to 1974. Only strong evidence that the 1974 year-class considerably exceeds 10^9 fish could justify a higher quota, since underestimation of year-class strength is equivalent to increasing the mean age of selection which, in this case, results in increased yield.

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An Evaluation of the Summer Flounder Population in Subarea 5 and Statistical Area 6¹

by

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ABSTRACT

An analysis of the summer flounder stock in Subarea 5 and Statistical Area 6 was made utilizing catch statistics and age-length and weight-length relationships. The stock exhibits an instantaneous total mortality rate of 0.56 to 0.69 for fully recruited ages. The estimates fishable population ranged from 36,000 to 74,000 metric tons from 1963 to 1974 and the MSY of 20,000 to 22,000 tons is approximately 6,000 tons lower than the estimated 1974 harvest of the commercial and recreational fisheries.

INTRODUCTION

This paper presents a preliminary assessment of the exploited stock of summer flounder, *Paralichthys dentatus*. It may serve both as a basis to develop a management scheme utilizing present survey information, and to evaluate the available data base for planning research studies.

The landed value of the summer flounder resource to United States commercial fishermen was in excess of 30 million dollars in 1974 (based on current values). The commercial fishery for summer flounder extends from southern New England to North Carolina in waters of less than 100 fathoms (Fig. 1). In New York most are taken by an inshore summer otter

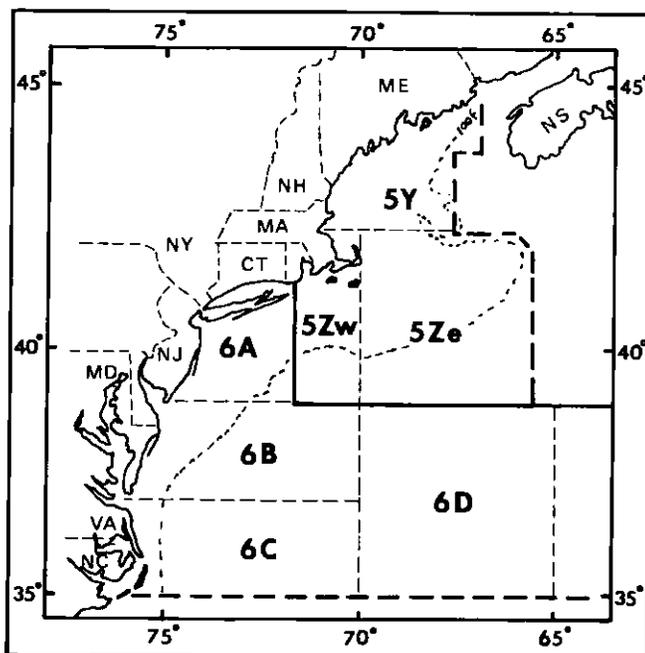


Fig. 1. Portion of the Atlantic coast showing locations of ICNAF Subarea 5 and Statistical Area 6.

¹ Submitted to the Twenty-fifth Annual Meeting, June 1975 as Res.Doc. 75/69.

trawl fishery off the south shore of Long Island. In New Jersey most are taken by a trawl fishery operating within 100 fm; summer (5-15 fm) and winter (40-80 fm). The summer inshore trawling catch has declined in recent years from a time when it was equal to the winter fishery. In Virginia the catch from the inshore summer trawl fishery usually exceeds that of the winter fishery with about 20% of the landed catch taken by pound nets in Chesapeake Bay. In North Carolina 90% of the catch is taken in a mixed trawl fishery operating in winter; the remainder is taken by fixed gear in estuarine waters during summer. In waters south of Chesapeake Bay the catch is reported in statistical summaries as "flounders" and comprises pleuronectid species other than *P. dentatus*.

The commercial nominal catches reported in ICNAF summaries are derived principally from United States monthly landing reports. The only other ICNAF statistics of summer flounder are provided by USSR and Canada.

The significance of the recreational fishery for summer flounder is shown in Fig. 2. The recreational catch statistics are derived from fisheries questionnaires of 1965 and 1970 United States population censuses (Deuel, 1973; Deuel and Clark, 1968); other data

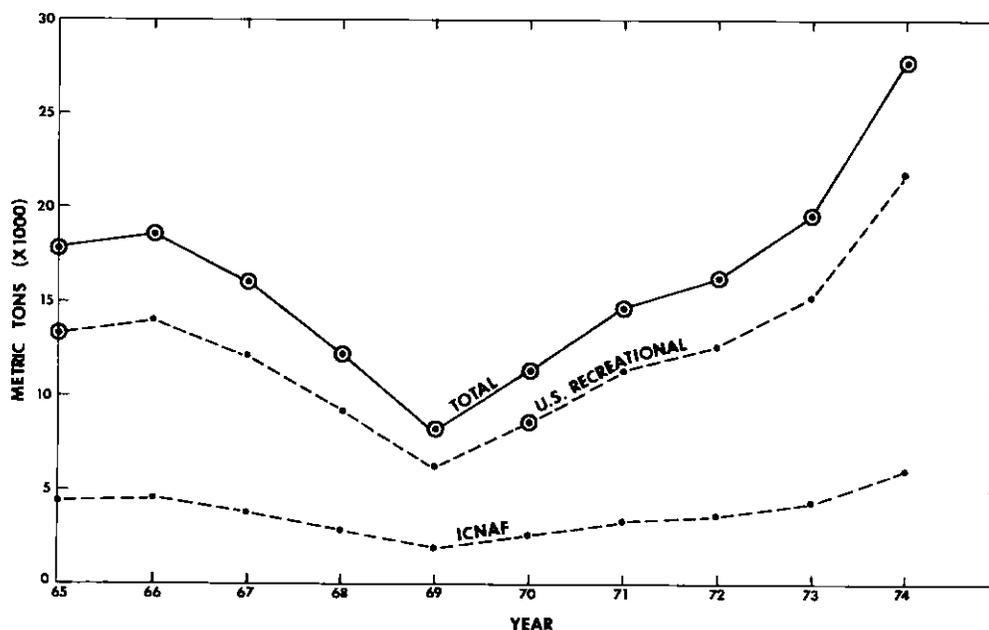


Fig. 2. Landings of commercial (ICNAF) and recreational fisheries for summer flounder, 1965-1974.

points are directly interpolated from the 1965 and 1970 angler catch ratio and the projected increase of the angler population. The recreational fishery is carried on by fishermen operating from shore and from private and chartered boats close to the coast. The most recent sport fishery survey (Deuel, 1973) indicates that approximately 750,000 anglers caught summer flounder, a 10% increase in effort from a similar survey 5 years earlier (Deuel and Clark, 1968).

Most resource survey statistics are based on semi-annual otter trawl research surveys by the Northeast and Middle Atlantic Coastal Fisheries Centers of the National Marine Fisheries Service (NMFS). No analysis was possible utilizing fishery effort data, because reliable statistics of the commercial and recreational effort do not exist. The gross effort of recreational participants in 1965 and 1970 are available but the data do not provide sufficient detail for analysis.

We have dealt with the stock identification problem by treating the Middle Atlantic population as a unit stock. There is some evidence to suggest that subgroups exist in the Middle Atlantic (Smith, 1973), although the time variation in availability of eggs and larvae essentially extends continuously from Block Island in November to North Carolina through April. However, R.W. Smith (personal communication) did not find sufficient evidence in meristic studies from North Carolina to Delaware to establish a basis for separate races or stocks. From tagging studies (Murawski, MS 1970; Poole, 1962) there

is some evidence of homing and considerable dispersal of older age-groups to the north-east in subsequent years. Summer flounder generally make an inshore migration in early spring from overwintering areas of 50 to 100 fm. There is evidence (Richards and Castagna, 1970) that the species moves from inshore shallows to cooler inlet and ocean waters during midsummer. There are differences in growth described in published studies (Eldridge, MS 1962; Poole, 1961; Smith, MS 1969), but Richards (1970) attributes variation in the New York data to a consistent ageing error.

In developing our estimates, biological information was incorporated with the reported nominal catch statistics (ICNAF *Statistical Bulletin*, Vol. 17-23, for the years 1967-1973), including appropriately weighted growth equations (Richards, 1970), age analysis of fluke from various regions (Eldridge, MS 1962; Poole, 1961; Smith, MS 1969) and unpublished file data of Messrs Paul Hamer, Walter Murawski and Patrick Festa (New Jersey Division of Marine Fish), Ronal Smith (University of Delaware) and Fred Lux (North-east Fisheries Center).

LANDINGS AND AGE-SIZE COMPOSITION

Since 1965, commercial nominal catches reported to ICNAF have varied annually from 1,900 to 6,100 tons. The low occurred in 1969 and the high in 1974 (Fig. 2). The 1965 and 1970 recreational catches were 13,400 and 8,700 tons respectively (Deuel and Clark, 1968; Deuel, 1973). Although the estimated angler catch data of Fig. 2 are interpolated, they reflect the increased catch of summer flounder by recreational fishermen in recent years. The proportionality of the angler catch increment ranged from an index of 3.0 in 1965 to 3.6 in 1974 with respect to commercial landings. A summary of United States commercial landings by State is given in Table 1. The northern segment of the commercial fishery had a persistent decline in landings from the early 1960's to a low in the early 1970's, whereas the southern portion maintained a consistent level. In recent years the total catch has increased to former levels (Fig. 2), but, without more reliable estimates of effort, it is impossible to relate this change to increased availability, intensified fishing, or increased population size.

Table 1. Annual USA commercial landings (000 pounds) of summer flounder by State. (Data from monthly landing reports, National Marine Fisheries Service.)

Year	Mass.	R.I.	Conn.	N.Y.	N.J.	Del.	Md. ¹	Va. ¹	Total
1950	3,613	1,036	270	3,838	2,514	25	(543)	(1,761)	13,601
1951	4,506	1,189	441	2,636	2,865	20	(327)	(2,006)	13,988
1952	4,898	1,336	627	3,680	4,721	69	(467)	(1,671)	17,470
1953	3,836	1,043	396	2,910	7,117	53	(1,176)	(1,838)	18,367
1954	3,363	2,374	213	3,683	6,577	21	(1,090)	(2,257)	19,578
1955	5,407	2,152	385	2,608	5,208	26	(1,108)	(1,706)	18,600
1956	1,448	1,604	322	4,260	6,357	60	(1,049)	(2,168)	21,289
1957	5,991	1,486	677	3,488	5,059	48	(1,171)	(1,692)	19,612
1958	4,172	950	360	2,341	8,109	209	1,452	2,039	19,632
1959	4,524	1,070	320	2,809	6,294	95	1,334	3,255	19,701
1960	5,583	1,278	321	2,512	6,355	44	1,028	2,730	19,851
1961	5,240	948	155	2,324	6,031	76	539	2,193	17,506
1962	3,795	676	124	1,590	4,749	24	715	1,914	13,587
1963	2,296	512	98	1,306	4,444	17	550	1,720	10,943
1964	1,384	678	136	1,854	3,670	16	557	1,492	9,787
1965	431	499	106	2,451	3,620	25	734	1,977	9,843
1966	264	456	90	2,466	3,830	13	630	2,343	10,092
1967	447	706	48	1,964	3,035	-	439	1,900	8,539
1968	163	384	35	1,216	2,139	-	350	2,164	6,451
1969	78	267	23	574	1,276	-	230	1,508	3,929
1970	41	259	23	900	1,958	-	371	2,146	5,698
1971	89	275	34	1,090	1,850	-	296	1,707	5,341
1972	70	276	-	1,101	1,852	-	277	1,856	5,432
1973	447	594	-	1,826	3,092	-	492	3,228	9,679
1974	1,600 ²	2,516 ²	-	2,481 ²	3,499	- ²	706 ²	2,733 ²	13,535

¹ Chesapeake Bay included; () indicates all "flounders".

² June-November.

Age composition of summer flounder (Fig. 3) was derived from trawl survey length data with an age-length table for the Delaware area (R. Smith, unpublished data). Two sets of data are shown: the longer set (from 1967) indicates results from surveys in waters from 15 to 200 fm; the shorter set (from 1972) incorporates results from surveys made in less than 15 fm depths. The shift in modal values to smaller sizes is explained in the calculated age composition profiles (Fig. 3) where an increase in the age 1 and 2 components was obtained from inshore catches. At least 10 age-groups made up the available population in recent years, 80-90% comprising age-groups 1-3. Based on survey statistics, there is some evidence that age-group 2 was fully recruited in recent years.

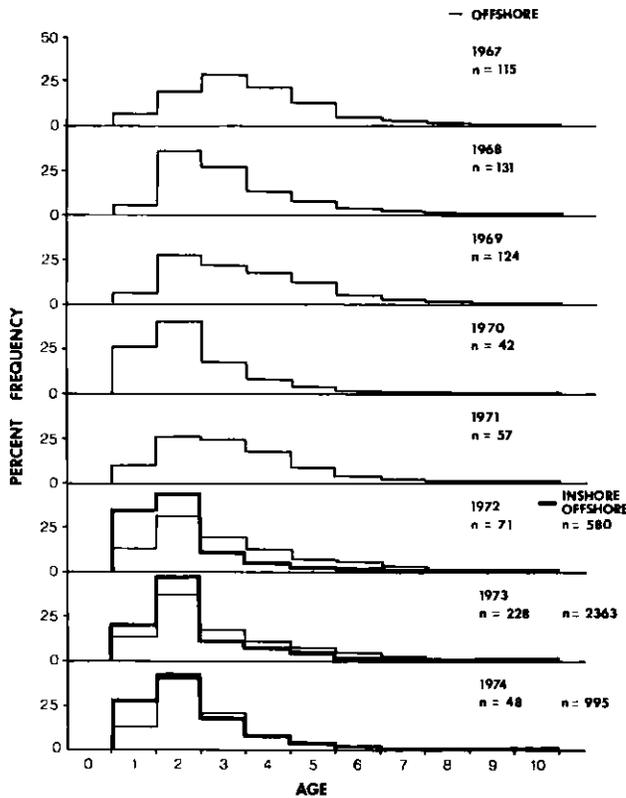


Fig. 3. Age composition of summer flounder available in Subarea 5 and Statistical Area 6. Offshore includes catches made in waters deeper than 15 fm. Inshore-offshore catches include those from shallower water surveys conducted since 1971.

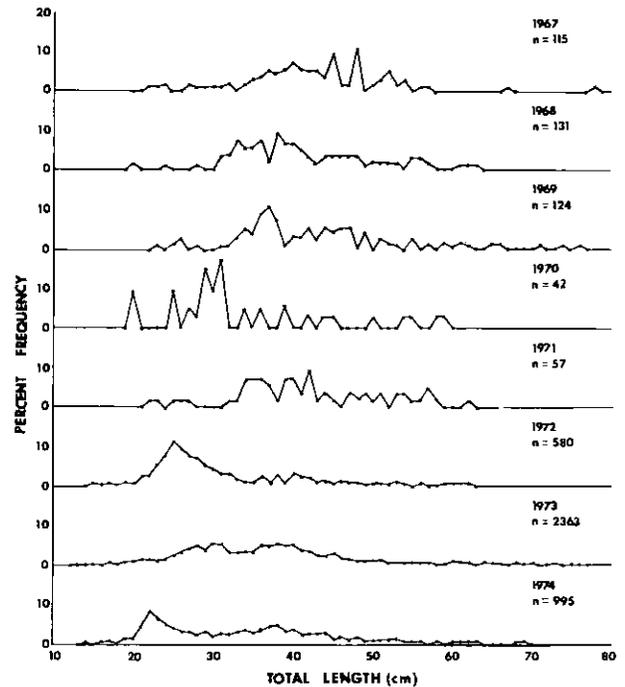


Fig. 4. Size distribution of summer flounder obtained by bottom trawl in Subarea 5 and Statistical Area 6.

The length distribution of summer flounder taken on groundfish surveys is given in Fig. 4. Lengths range from 12 to 80 cm. Since 1967, modal lengths have decreased from the mid-40 cm to a current range in the mid-20 cm groups. The discontinuous distributions of earlier years (1967-1971) are due to smaller sample sizes. A higher proportion of smaller fish in the pooled length composition in recent years (1972-1974) has probably resulted from both increased survey activity in shallower waters and increased recruitment.

ESTIMATION OF POPULATION PARAMETERS

Mortality Rate

Of the several methods for estimating mortality in fish populations, those most applicable to the present study include age composition, cohort analysis and tagging data analysis. Age composition analysis involves estimation of the rate of decline of abundance with increasing age, i.e. $\ln(C_i) = a - Zi$, where C_i is catch at age i , a is a constant and

Z is instantaneous total mortality. The virtual population method (Gulland, MS 1965) provided a set of instantaneous fishing mortality rates summarized in Table 2. Estimates of fishing and natural mortality rate, including an additional mortality factor due to the tags, were obtained by Paulik's method (1963). Results of the tagging analysis are based in part on the numbers of released and recaptured tags of NMFS experiments at Point Judith, Rhode Island and Nantucket Sound in 1962. Additional tagging data were analysed from published reports of Poole (1961) and Murawski (MS 1970).

Table 2. Estimated instantaneous fishing mortality rates (F) for summer flounder by virtual population method with instantaneous natural mortality, $M = 0.2$, and total instantaneous mortality rates, Z, estimated by $\ln(C_i) = a - Zi$, where C_i is catch of age i.

Year	Age										F ¹ (2-10)	Z
	1	2	3	4	5	6	7	8	9	10+		
1967	0.051	0.212	0.472	0.637	0.615	0.556	0.527	0.705	0.569	0.5	0.533	0.62
1968	0.036	0.383	0.460	0.402	0.436	0.434	0.482	0.647	0.744	0.5	0.499	0.59
1969	0.180	0.133	0.237	0.304	0.405	0.320	0.301	0.350	0.397	0.5	0.327	0.60
1970	0.146	0.386	0.306	0.300	0.263	0.290	0.369	0.469	0.551	0.5	0.382	0.56
1971	0.024	0.154	0.307	0.414	0.445	0.345	0.406	0.603	0.863	0.5	0.449	0.58
1972	0.247	0.611	0.335	0.337	0.350	0.392	0.239	0.355	0.414	0.5	0.393	0.67
1973	0.099	0.461	0.374	0.368	0.494	0.417	0.351	0.296	0.413	0.5	0.408	0.69

¹ Average fishing mortality of ages 2-10.

The differences in estimates of instantaneous fishing mortality rate (F) appear to be insignificant over the time period analyzed (Table 2). Compared with these values, estimates derived from earlier tagging experiments (Table 3) do not suggest any long-term trend changes. F values did not consistently change as landings changed.

Table 3. Summary of estimated instantaneous fishing and natural mortality rates from tagging experiments by various sources.

Study	Source	Location	Tag type	χ^1	F
1956	Poole (1961)	Long Island, N.Y.	Petersen	0.91	0.50
1961	Hamer (unpubl.) and Murawski (1970)	Sandy Hook, N.J.	Petersen	0.84	0.37
			Atkins	0.97	0.34
1962	Lux (unpubl.)	Point Judith, R.I. Nantucket, Mass.	Petersen	0.57	0.55
			Petersen	0.77	0.52

¹ Includes both natural mortality and lose due to tagging.

In the observed period, as judged from calculated F values, year-classes are fully recruited to the fishery at age 2 or 3, and the mortality of the Middle Atlantic Bight summer flounder at ages 2-3 is not greater than that of ages 4-10. This may indicate that mortalities of the newly recruited age-groups are not receiving the full impact of fishing mortality upon their entry into the fishery.

The estimates of instantaneous total mortality rates (Z) fall in a range from 0.56 to 0.69 (Table 2), estimated by age composition analysis. Compared with the values from the virtual population procedure, some indication of differences appear to exist between the two sets of mortality rates. The reason for this is not clear, but, since the summer flounder population in the Middle Atlantic Bight is not in steady state and the role of the recreational fishery is such a dominant factor, the assumptions implied by the catch curve analysis have apparently been violated.

The estimate of the instantaneous natural mortality rate (M) is only available from the tagging experiments, since we do not have any reliable set of effort data to plot against total mortality rates. Three independent experiments led to somewhat different sets of M values ranging from 0.57 to 0.97. These appear to be high; however, considering the conditions of releasing fish, the few tag returns from fishermen in some areas,

the tagging mortality, and higher vulnerability of Petersen-type tags to the fishing nets, these estimates are reasonable. The X values are only provisionally acceptable figures, considering the natural mortality of other flounders (Beverton and Holt, 1959; Lux, 1969). A more realistic estimate of M for summer flounder may be around 0.2. The remaining portion of X values may be considered mortality due to the variabilities related to tagging experiments and the tag itself.

An interesting observation in the Middle Atlantic summer flounder population is the scarcity of 5- and 6-year-old males and the absence of any older than age 7 (Eldridge, MS 1962; Poole, 1961; Smith, MS 1969). Thus, the natural mortality rate of male summer flounder must increase dramatically beyond ages 4 and 5.

Recruitment Rate

Table 4 summarizes recruitment rates for the Middle Atlantic Bight summer flounder, using Allen's method (1966), under the assumptions of M = 0.2 and that the total mortality rates for fully and partially recruited ages are the same. With the assumption of M being constant, only the effects of fishing mortalities of newly recruited and fully recruited fish are considered. In recent years the age of full recruitment is younger than in earlier years. The fully recruited age for the Middle Atlantic Bight summer flounder is 3 years for 1967-1972 and 2 years for 1973-1974.

Table 4. Estimated recruitment rate for summer flounder under the assumption of M = 0.2 and total mortality for fully recruited and newly recruited fish is the same (i.e. $Z = Z^1$).

Year	Recruitment rate ¹	Age			W _t ²
		2	3	4-10	
1967	U	0.60	1.00	1.00	
	R	+	+	+	
	W	+	+	+	+
1968	U	0.96	1.00	1.00	
	R	1.00	0.44	0.00	
	W	0.36	0.12	0.00	0.48
1969	U	0.61	1.00	1.00	
	R	1.00	0.62	0.00	
	W	0.27	0.15	0.00	0.42
1970	U	0.79	1.00	1.00	
	R	1.00	0.20	0.00	
	W	0.40	0.03	0.00	0.43
1971	U	0.81	1.00	1.00	
	R	1.00	0.28	0.00	
	W	0.27	0.07	0.00	0.34
1972	U	0.82	1.00	1.00	
	R	1.00	0.39	0.00	
	W	0.44	0.04	0.00	0.48
1973	U	1.00	1.00	1.00	
	R	1.00	0.20	0.00	
	W	0.47	0.03	0.00	0.50
1974	U	1.00	1.00	1.00	
	R	1.00	0.16	0.00	
	W	0.41	0.03	0.00	0.44

¹ U = proportion of recruits in each age-group; R = proportion of new recruits in the recruited part of each year-class; W = proportion of new recruits in the exploited stock in each age-group.

² W_t = total proportion of new recruits in the exploited stock for the year t. + = not computable as 1966 catch data for each age-group is not available.

An interesting aspect of the recruitment rate is shown in Table 4. There is an increasing proportion of new recruits in the exploited population in the 2-year-old age-group; however, the total proportion of new recruits in the exploited population has not shown comparable increases in recent years. Table 4 also indicates that at least 40-50% of the newly recruited summer flounders in the Middle Atlantic Bight had not reached the threshold maturity age of 3 years. Therefore, an adverse effect on the reproductive capacity is indicated.

Growth

The growth in length and weight of the Middle Atlantic Bight summer flounder has been investigated by Eldridge (MS 1962), Lux and Porter (1966), and Smith (MS 1969). Poole (1961) studied growth in length of summer flounder in the Great South Bay, Long Island. Richards (1970) re-examined Poole's data using analog computer simulation and found a better fit when the lengths were shifted to a point 1 year older than that as given (Table 5). Using this correction, he developed Bertalanffy's growth equation for summer flounder as follows:

$$\begin{aligned}
 \text{Males: } l_t &= 607 \left(1 - e^{-0.240(t+0.11)} \right) \\
 w_t &= 2608 \left(1 - e^{-0.214(t+0.02)} \right)^{2.8} \\
 \text{Females: } l_t &= 943 \left(1 - e^{-0.164(t+0.1)} \right) \\
 w_t &= 13431 \left(1 - e^{-0.144(t+0.04)} \right)^{3.2}
 \end{aligned}$$

Table 5. Comparison of published mean length-at-age data (mm) for male and female summer flounder.

	Age 1		Age 2		Age 3		Age 4		Age 5		Age 6	
	M	F	M	F	M	F	M	F	M	F	M	F
Poole (1951)	271	251	377	326	455	387	-	-	-	-	-	-
Eldridge (1962)	-	-	-	-	375	320	425	355	478	385	515	403
Smith (1969)	-	-	279	256	387	345	460	403	512	449	568	-
Richards (1970)	156	142	275	241	376	319	462	381	528	429	-	-

The units are in millimeters for the length and grams for the weight. Using these same criteria, Eldridge's data for 3-year-old fish agree with Richards' equation, but fish over 5 years old should be shifted back 1 year (i.e. read as 1 year younger) for agreement. Smith's estimates are in agreement with those of Richards (Table 5).

Some clarification of ageing is necessary. Confounding elements within a single population may include growth variations, relation of maturity to annulus formation, and variations in the time of annulus formation; or the samples may have come from separate populations. These equations show the rate of growth in weight and length for males is greater than that of females, although theoretical maximum length and weight of females is much greater than those of males. The male values of L_∞ and W_∞ correspond to the scarcity of older male summer flounder in the fishery, i.e. male summer flounder grow faster and die out at a younger age than females.

ESTIMATION OF POPULATION SIZE

Since a good index for effective fishing effort is not available and availability of fish may fluctuate considerably from year to year, there may be considerable error involved in the age composition method of estimating mortality rates. To avoid such marked effects of changes in availability, Fry (1949) used virtual population estimates in place of abundance. Chapman (MS 1958), Gulland (MS 1965), and Pope (1972) modified this method to estimate population sizes more easily. Tables 6 and 7 summarize the estimated Middle Atlantic Bight summer flounder population size by year-class obtained using MEFC's computer program based on Gulland's method.

Table 6. Estimated summer flounder population size in numbers (000 fish) by year-classes from 1967 to 1974.

Year	Year-class													Population size total		
	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970		1971	1972
1967	425	724	1,341	2,581	5,962	10,091	15,589	22,129	28,727	-	-	-	-	-	-	87,569
1968	198	293	648	1,212	2,639	4,370	7,963	14,658	22,354	30,387	-	-	-	-	-	84,722
1969	-	114	278	613	1,400	2,314	4,361	7,579	12,482	23,999	41,641	-	-	-	-	94,781
1970	-	-	153	354	848	1,377	2,382	4,580	8,059	17,209	33,515	51,909	-	-	-	120,386
1971	-	-	-	167	435	780	1,459	2,883	4,887	10,380	18,644	36,738	82,187	-	-	158,560
1972	-	-	-	-	150	349	796	1,672	2,565	5,617	11,232	25,785	65,715	111,438	-	225,319
1973	-	-	-	-	-	189	457	1,078	1,419	3,242	6,568	15,097	29,193	71,239	111,926	247,750
1974	-	-	-	-	-	-	248	656	818	1,749	3,282	8,557	16,436	36,771	88,405	156,922

Table 7. Estimated summer flounder population size in weight (metric tons), and total landings in weights from commercial and recreational fishes.

Year	Year-class													Population size (m tons)	Total catch (m tons)		
	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970			1971	1972
1967	2,067	2,884	4,002	5,446	8,192	8,174	6,469	3,430	718	-	-	-	-	-	-	41,382	16,104
1968	1,188	1,425	2,582	3,617	5,568	6,004	6,450	6,083	3,465	760	-	-	-	-	-	37,142	12,256
1969	-	684	1,352	2,442	4,178	4,883	5,992	6,139	5,180	3,720	1,041	-	-	-	-	35,611	8,233
1970	-	-	918	1,722	3,378	4,109	5,026	6,293	6,528	7,142	5,195	1,298	-	-	-	41,609	11,421
1971	-	-	-	1,002	2,115	3,108	4,354	6,083	6,715	8,408	7,737	5,694	2,055	-	-	47,271	14,777
1972	-	-	-	-	900	1,697	3,171	4,989	5,412	7,718	9,098	10,701	10,186	2,786	-	56,658	16,343
1973	-	-	-	-	-	1,134	2,223	4,295	4,234	6,841	9,024	12,229	12,115	11,042	2,982	66,119	19,720
1974	-	-	-	-	-	-	1,448	3,190	3,259	5,219	6,925	11,757	13,313	15,560	13,703	74,374	37,995

Estimated population size in numbers (Table 6) progressively increased in the observed period by a factor of 2.8 from 80 million in 1967 to 247 million in 1973. The fishable population size in weight (Table 7) increased by a factor of 1.6 during the same interval, from 41,000 to 66,000 tons. This reflects an increased number of younger fish in the estimates which do not have a proportionate increment in weight. Thus, recent summer flounder population estimates include more younger fish than those of earlier years.

The estimated population in 1974 does not include the 1-year-old age-group, so numbers are less than that of 1973. However, the population weight is larger than that of 1973. This reflects the influence of strong year-classes of 1970, 1971, and 1972 prevailing into the 1974 population weight, since the net weight contribution of these stronger year-classes to the 1974 population is greater than those of the 1973 population.

YIELD ANALYSIS

Besides the two most popular methods of yield analysis, the dynamic pool model with yield per recruit analysis and the surplus yield model with general production equation, more recent developments of yield analysis have been accomplished by Chapman (MS 1970) and Doi (1972). Their designs have employed a reproduction mechanism to obtain the level of sustainable yield and population size.

Doi's mathematical formulations may be modified for the Middle Atlantic Bight summer flounder fishery as follows: let R be the number (or index) of recruits at age 1, let $s = e^{-(F+M)}$ be the annual rate of survival, and let t_c be the first age of entry to the fishery. We may assume that average maturity for summer flounder occurs at age 3, since Smith (MS 1969) observed the smallest male caught with ripening testes was 305 mm long and the smallest female with ripening ovaries was 390 mm long. The ages of those male and female fish were 3 years old based on an age-length table constructed from his data. From Richards' equation (1970), male lengths correspond to ages $2 < t \leq 3$ and females $3 \leq t < 4$.

The fishable stock size N (ages 1-10) and the spawners S are then, for $t_m = 3$ and $t_c = 1$,

$$N = \frac{R (1 - s^{11})}{1 - s} \text{ and } S = \frac{R s^2 (1 - s^9)}{1 - s}$$

and so the reproduction rate (K) can be written as

$$K = \frac{R}{S} = \frac{1 - s}{s^2 (1 - s^9)}$$

For $t_m = 3$ and $t_c = 2$, we have $N = \frac{R s_0 (1 - s^{10})}{1 - s}$ where $s_0 = e^{-M}$.

Have $S = \frac{R s_0 s (1 - s^9)}{1 - s}$ and $K = \frac{R}{S} = \frac{1 - s}{s_0 s (1 - s^9)}$.

Although K values are easily obtainable, there is no analytical solution for s . We computed K 's with s 's and plotted K 's on s 's (Fig. 5) for various t_c values within $t_m = 3$. With this plot, summer flounder survival rates can be estimated from known reproduction rates.

Tables 8 and 9 represent calculations of sustainable yield for the Middle Atlantic Bight summer flounder fishery with reference to its spawner-recruit relationship and estimated parameters described above and in Fig. 5. These computations are treated with values of $t_c = 1$ and 2; $t_m = 3$ and a constant $M = 0.2$. Then the maximum sustainable yield (MSY) both in numbers and weights are observed at a spawner index, $S = 3.0$. The MSY in weights (Y_s) are 20,000 and 22,000 tons with fishing intensity (F) of 0.45 and 0.69 and average weight per fish (W) 562 and 674 grams for $t_c = 1$ and $t_c = 2$ respectively.

The present level of the estimated 1974 landings from commercial and recreational fisheries is larger than the MSY level of 20,000-22,000 tons.

The 8 years of data points (1967-1974) generate only 6 points for a spawner-recruit relationship, since there is a 2-year time lag effect of spawners to recruits. Thus, under the circumstances, determination of this relationship is particularly meager in extrapolating from 6 given points. However, it is the only way to obtain MSY without utilizing the effective effort statistics.

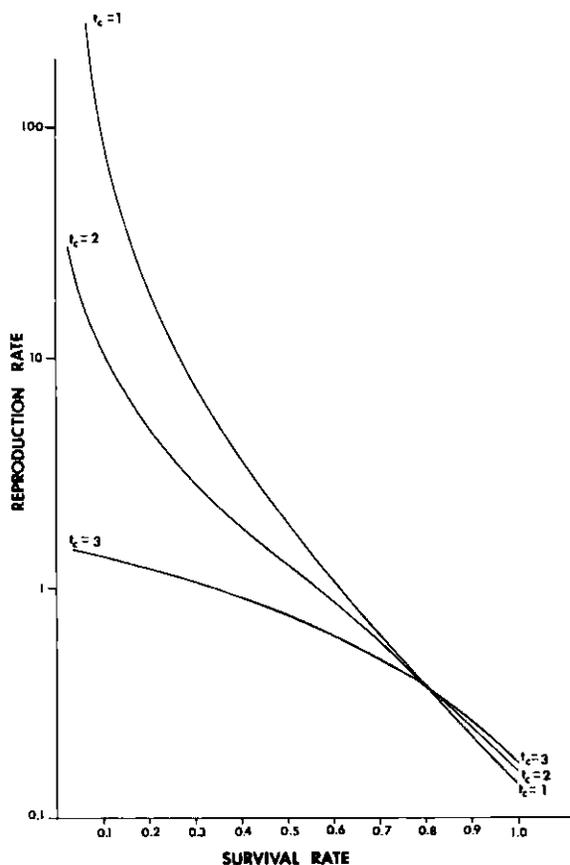


Fig. 5. Relationship between reproduction rates and survival rates under the assumption of maturity age $t_m = 3$, and with the various ages entering the fishery $t_c = 1, 2$, and 3 .

Table 8. Sustainable yields in numbers and weights for the summer flounder population with spawner-recruit relationships calculated under the assumptions of $M = 0.2$, $t_m = 3$, $t_c = 1$, and $\bar{w} = 562$ grams.

S (10^{-7})	R (10^{-7})	K	s	Z	F	E	N (10^{-7})	C (10^{-7})	P (tons)	Y (tons)
0.1	0.35	3.50	0.41	0.89	0.69	0.46	0.59	0.27	3316	1517
0.5	1.59	3.18	0.43	0.84	0.64	0.43	2.79	1.20	15680	6744
1.0	2.81	2.81	0.45	0.80	0.60	0.41	5.11	2.09	28718	11746
2.0	4.40	2.20	0.49	0.71	0.51	0.37	8.62	3.19	48444	17928
3.0	5.17	1.72	0.52	0.65	0.45	0.33	10.76	3.55	60471	19951
4.0	5.40	1.35	0.57	0.56	0.36	0.28	12.53	3.51	70419	19726
5.0	5.28	1.06	0.61	0.49	0.29	0.23	13.48	3.10	75758	17422
6.0	4.96	0.83	0.65	0.43	0.23	0.19	14.17	2.69	79635	15118
7.0	4.53	0.65	0.70	0.36	0.16	0.13	14.80	1.92	83176	10790
8.0	4.05	0.51	0.74	0.30	0.10	0.16	15.01	1.50	84356	8430
9.0	3.57	0.40	0.79	0.24	0.04	0.03	15.73	0.47	88403	2641
10.0	3.11	0.31	0.83	0.19	-	-	-	-	-	-

S = spawners (index or number)

R = recruits (index or number)

K = reproduction rate

s = survival rate

Z = $-\ln(s)$

F = $Z-M$

$$E = \frac{F}{Z} (1-s)$$

$$N = \frac{R \cdot S_0(1-s^{10})}{1-s}$$

$$C_s = NE$$

$$P = N\bar{w}$$

$$Y_s = C_s \cdot \bar{w}$$

Table 9. Sustainable yield in numbers and weights for the summer flounder population with spawner-recruit relationships calculated under the assumptions of $M = 0.2$, $t_m = 3$, $t_c = 2$, and $\bar{w} = 674$ grams.

S (10^{-7})	R (10^{-7})	K	s	Z	F	E	N (10^{-7})	Gs (10^{-7})	P (tons)	Ys (tons)
0.1	0.35	3.50	0.26	1.35	1.15	0.63	0.39	0.25	2627	1685
0.5	1.59	3.18	0.28	1.27	1.07	0.61	1.81	1.01	12199	6807
1.0	2.81	2.81	0.30	1.20	1.00	0.58	3.29	1.91	22175	12873
2.0	4.40	2.20	0.35	1.05	0.85	0.53	5.54	2.94	37340	19815
3.0	5.17	1.72	0.41	0.89	0.69	0.46	7.17	3.30	48326	22242
4.0	5.40	1.35	0.48	0.73	0.53	0.38	8.50	3.23	57290	21770
5.0	5.28	1.06	0.54	0.62	0.42	0.31	9.38	2.91	63221	19613
6.0	4.96	0.83	0.61	0.49	0.29	0.23	10.34	2.38	69692	16041
7.0	4.53	0.65	0.67	0.40	0.20	0.17	11.09	1.88	74747	12671
8.0	4.05	0.51	0.73	0.31	0.11	0.10	11.75	1.18	79195	7953
9.0	3.57	0.40	0.79	0.24	0.04	0.03	12.60	0.38	84924	2561
10.0	3.11	0.31	0.83	0.19	-	-	-	-	-	-

DISCUSSION AND RECOMMENDATIONS

A critique of the assumptions leading to our various conclusions is useful to point out where and why certain analytical elements should be enhanced.

In the stock identification, we have made the assumption of a unit stock. At present this is an allowable premise, based on the progression of spawning (Smith, 1973) and a relatively homogeneous availability to the fisheries. R.W. Smith (personal communication) reports that he found insufficient evidence in meristic studies from North Carolina to Delaware to establish any separate races or stocks. Oceanographic and other factors may affect annual survival in different geographic sections of the fishery and a regional catch composition analysis would demonstrate their characteristics and whether persistent differences occur. A discriminate function analysis of area samples could also evaluate the validity of our premise.

Data used in the age-length analysis were derived only from Delaware Bay samples (R. Smith, personal communication). Although, because of its geographic location, it may be assumed to reflect a central characteristic, a larger sample with greater coverage would allow a more representative estimate over the species range in Middle Atlantic waters. Strategic timing of survey cruises could also contribute to more representative sampling of the resource.

A detailed set of effort statistics would allow more flexibility in analysis, specifically to allow a Schaefer model to be generated. To this end, we would suggest a State-Federal effort in obtaining such statistics, and a standardization of sampling nets to ensure results from the Middle Atlantic resource surveys could also be used as consistent source data for such an analysis. For a first-level approximation, some effort should be applied to develop catchability characteristics of the nets currently in use. An experiment should be designed to evaluate relative effectiveness of trawls variously rigged with rollers, discs and chain sweeps.

The historical summary of landings shows the commercially harvested fraction is dwarfed by the influence of a significant recreational fishery. Statistical sources do not contain paired estimates of commercial and recreational landings. Furthermore, the entry for summer flounder is often lost in a statistical clustering of "flatfish" or "other flounders". A series of synoptic surveys addressing the problem of effort landings and age characteristics from both commercial and recreational landings would appear to be a proper objective of a State-Federal program.

From our preliminary analysis, we have concluded that the fishable population is one characterized by a stock fully recruited by age 3 and in recent years dominated by modal age-groups of 2 or 3. A trend of increasing harvest in recent years appears to have resulted from a series of strong year-classes from 1970 to 1972. Development of a spawner-recruit curve and yield analysis suggest a sustainable catch level of 20,000-22,000 tons in the Middle Atlantic Bight. However, this value could fluctuate in response to changes in future recruitment. The 1974 combined fishery harvest of 27,000 tons is greater than our estimate of a sustainable yield.

This study should be updated and improved with the acquisition of new information, primarily from areas suggested. It essentially presents an imminent problem situation and suggest the integration of angler catches in landing estimates is a factor not to be ignored. Quality reporting and real time feedback from survey and biological studies are a continuing and real need for development of conservation schemes in maintaining the viability of the summer flounder fishery.

SUMMARY

This study is a first analysis of the population dynamics of summer flounder, incorporating recreational and commercial catches of the Middle Atlantic coastal shelf. The population is fully recruited to the fishery at ages 2 to 3 and the total instantaneous mortality rate ranges from 0.56 to 0.69. The length and weight relationships to age indicate that the growth rate for males is greater than for females, but the maximum size of females is greater. Estimated fishable populations have varied from 80 to 247 million between 1963 and 1974. More young fish have been harvested in recent years. Estimated maximum sustainable yield is 20,000-22,000 tons, lower than the calculated combined catch (commercial and recreational) of 27,000 tons calculated for 1974.

ACKNOWLEDGMENTS

We appreciate the cooperative response from colleagues in satisfying our need for information. In addition to supplying data, editorial comments were obtained from researchers of summer flounder at the Northeast Fisheries Center, the New York Division of Marine and Coastal Resources, the New Jersey Division of Fish, Game and Shellfish, the University of Delaware's College of Marine Studies, the Virginia Institute of Marine Science, and the South Carolina Marine Resource Research Institute. At the Middle Atlantic Coastal Fisheries Center, Messrs Thomas Azarovitz, Wallace Smith and Stuart Wilk made helpful comments on earlier drafts.

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Distribution and Relative Abundance of Roundnose, Roughhead and Common Grenadiers in the Northwest Atlantic¹

by

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ABSTRACT

This paper provides information on research catches of roundnose (*Coryphaenoides rupestris*), roughhead (*Macrourus berglax*) and common (*Nezumia bairdii*) grenadiers in the Canadian area of the Northwest Atlantic in relation to area, depth and temperature.

Roundnose grenadiers are most plentiful in deep water on the continental slope in ICNAF Divisions 3K, 2J and off the northern third of Labrador at bottom temperatures of 3.5 to 4.5°C. Largest catches were obtained at depths greater than 275 fathoms (503 metres). More than 80% of commercial roundnose grenadier catches has been taken in Div. 3K, with largest catches during June-October. The maximum sustainable yield of roundnose grenadiers in Subareas 2 and 3 has been estimated at 24,000-37,000 metric tons. To date, the fishery has exploited only concentrations of immature fish which are now apparently fully exploited. The potential of the total stock may be substantially higher if the fishery were extended to mature fish at greater depths.

Largest research catches of roughhead grenadiers were obtained along the eastern edge of the Grand Bank (Div. 3L and 3N), at depths of 100 to 275 fm (183 to 503 m) and bottom temperatures between 2.0 and 3.5°C. Maximum catch rates of roughhead grenadiers were considerably less than maximum catch rates of roundnose grenadiers.

Catches of common grenadiers were very small in all areas fished, generally less than 5 kg per 30-minute set, generally at bottom temperatures from 3.0 to 5.0°C. Because of its limited biomass and small size (generally 0.1-0.2 kg) the common grenadier is unsuitable for commercial exploitation.

INTRODUCTION

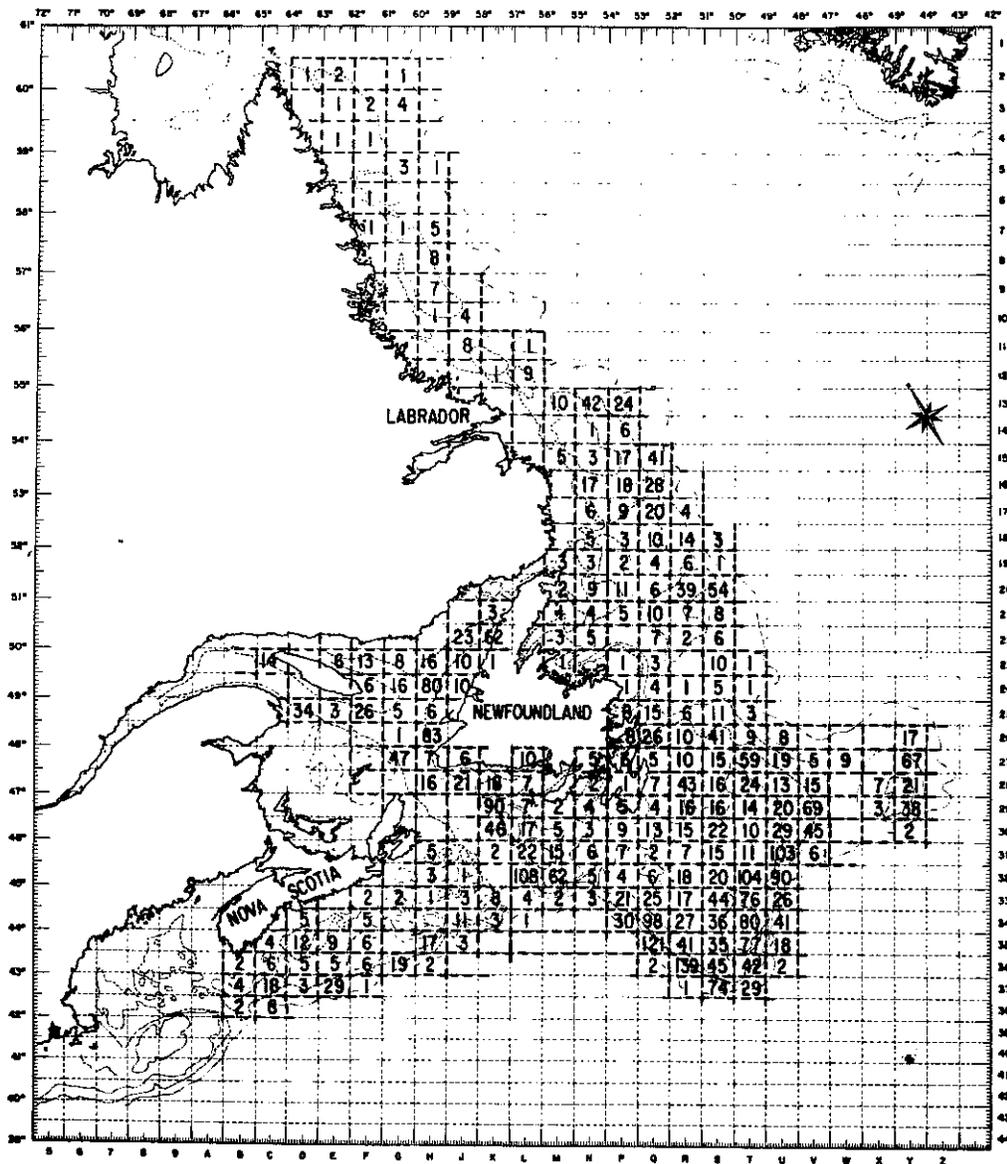
Grenadiers, fishes of the family Macrouridae, are deep-water species, most of which dwell on the continental slopes. At least seven species have been reported to occur off the Canadian Atlantic coast. Only three of these - the roundnose (*Coryphaenoides rupestris* Gunnerus 1765), roughhead (*Macrourus berglax* Lacépède 1802) and common (*Nezumia bairdii* Goode and Bean 1877) - are plentiful and only one, the roundnose, is presently being exploited to any extent, chiefly by the USSR.

This paper presents information on research catches of roundnose, roughhead and common grenadiers in the Canadian area of the Northwest Atlantic in relation to area, depth and temperature and also reviews some aspect of the biology of these species. For taxonomic descriptions and distinctions, see Marshall and Iwamoto (1973).

¹ Submitted to 1975 Annual Meeting as Res.Doc. 75/26.

MATERIALS AND METHODS

The information on distribution and relative abundance of the three grenadier species in relation to area, depth and temperature was obtained from the catches of the 168-foot Canadian research vessel *A.T. Cameron* during 1958-73. Only data from survey otter trawling sets of the *A.T. Cameron*, using a no. 41-5 Yankee otter trawl (24.1 m headrope), towed usually at 3½ knots for 30 minutes, were used. All survey sets were at positions unselected for abundance of grenadiers. Numbers of successful fishing sets per ½ degree latitude by 1 degree longitude rectangle are given in Fig. 1. Fishing sets extended from the shallowest water of the banks to about 400 fm (730 m) on the slopes and very occasionally deeper. Otter trawling on the slopes was generally carried out on a depth contour at predetermined depths in fathoms.



DISTRIBUTION BY AREA

Roundnose grenadier

Research vessel catches of roundnose grenadiers were restricted to deep water at the seaward edge of the continental shelf. Catches were greatest on the eastern edge of Funk Island Bank (Div. 3K), on the edge of Hamilton Inlet Bank (Div. 2J) and off the northern third of Labrador (Fig. 2 and 3). Some good catches were obtained in deep water on the western side of Davis Strait (Fig. 4). Only small quantities were obtained in deep water on the edge of the Flemish Cap, Grand Bank and St. Pierre Bank. The species was absent in the Gulf of St. Lawrence; a few specimens were taken in deep water on the seaward slope of the Scotian Shelf.

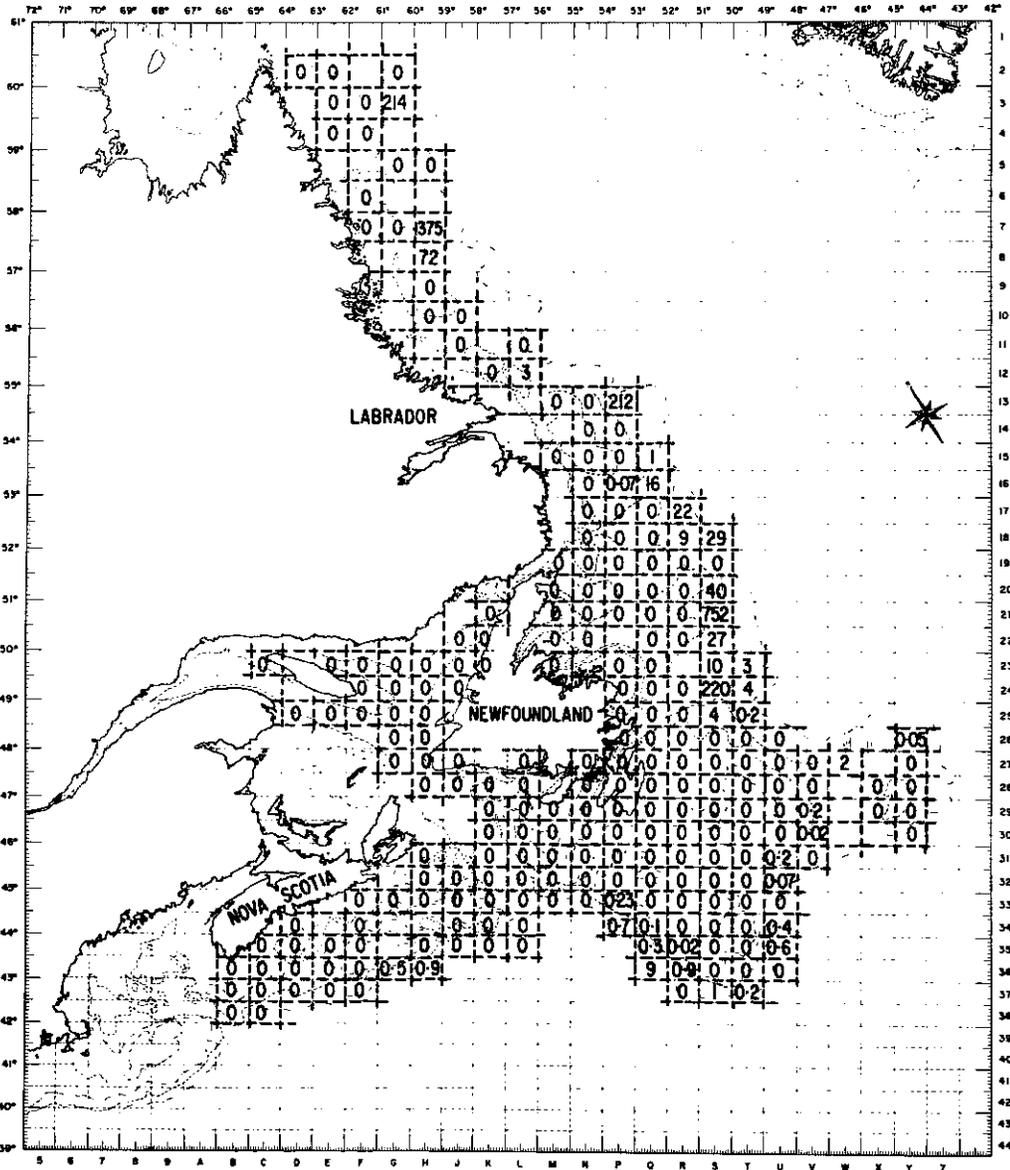


Fig. 2. Average catch of roundnose grenadier, kg whole weight, by 1/2 degree latitude, 1 degree longitude rectangle per 30-minute on bottom otter-trawling set of the A.T. Cameron during 1958-73.

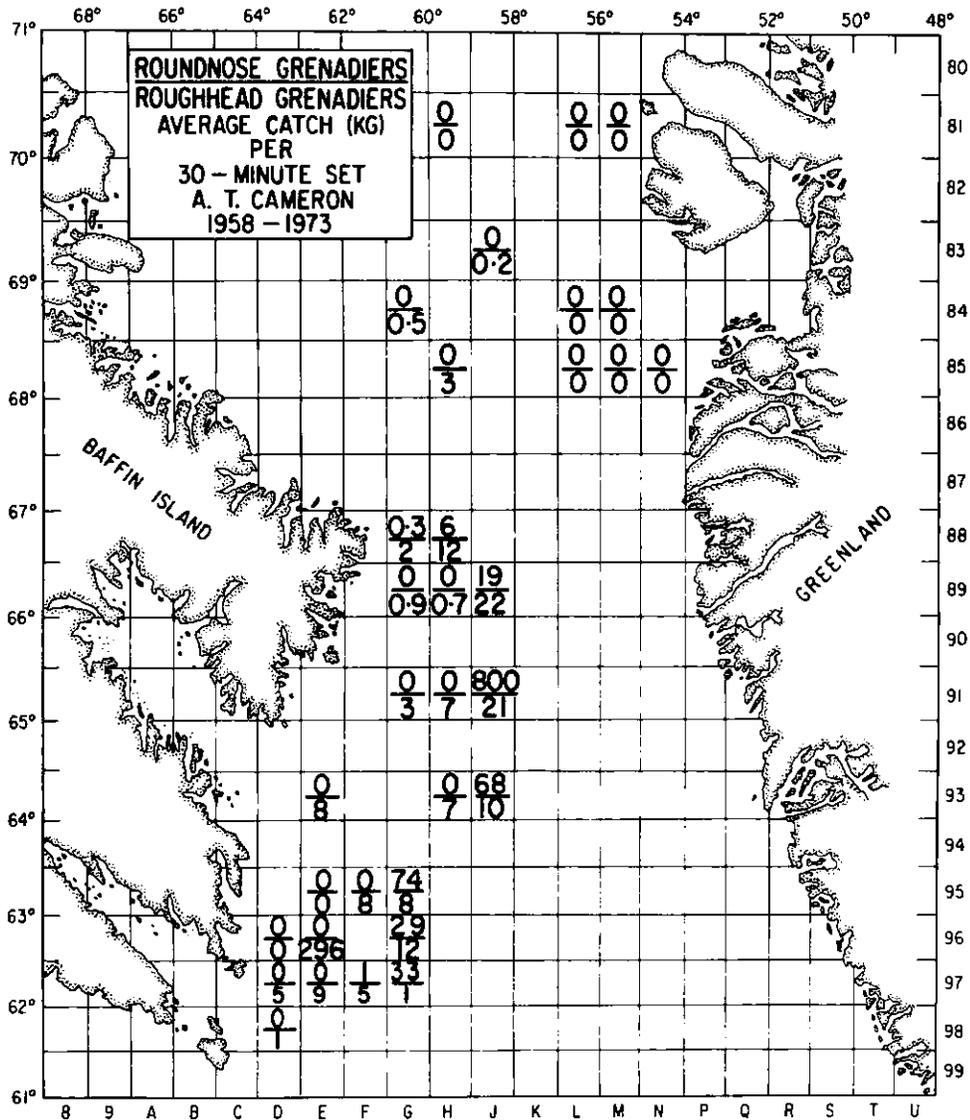


Fig. 4. Average catches of roundnose and roughhead grenadiers, kg whole weight, by ½ degree latitude, 1 degree longitude rectangle per 30-minute on bottom otter-trawling set of the A.T. Cameron in the Baffin Island-Greenland area.

Roughhead grenadier

The roughhead grenadier appears to be somewhat more widely dispersed than the roundnose. Greatest catches of roughheads were obtained along the eastern edge of the Grand Bank (Div. 3L and 3N) where maximum catches of 343 and 544 kg per 30-minute tow were obtained (Fig. 5 and 6). Good catches were also obtained off northern Labrador and Baffin Island where maximum catches of 69-94 and 296 kg per 30-minute set were obtained. Catches in the area from Hamilton Bank to Funk Island Bank (maximum catches of 30-60 kg per 30-minute set) were intermediate between those to the south and the north. Moderate catches of roughhead grenadiers were obtained on the northeast Newfoundland Shelf in the Funk Island Bank and Deep areas, but the species was absent on the shallower portions of the Grand Bank, in Div. 3P, in the Gulf of St. Lawrence and on the Scotian Shelf, with only a few specimens taken on the seaward slope of the Scotian Shelf. Maximum catches of roughhead grenadiers in ½ degree latitude by 1 degree longitude rectangles where they were most abundant were considerably less than the maximum catches of roundnose grenadiers in areas where they were most abundant.

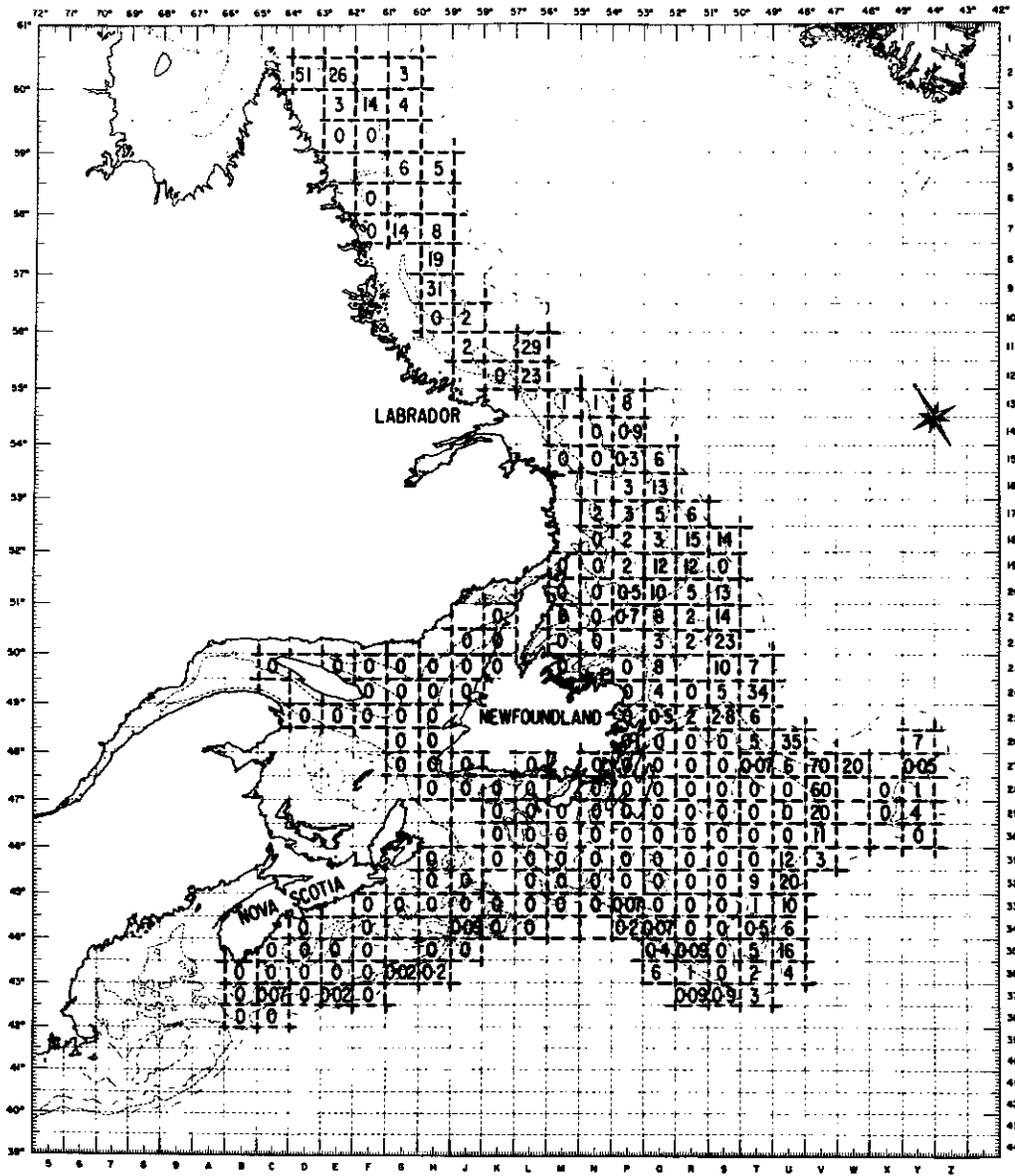
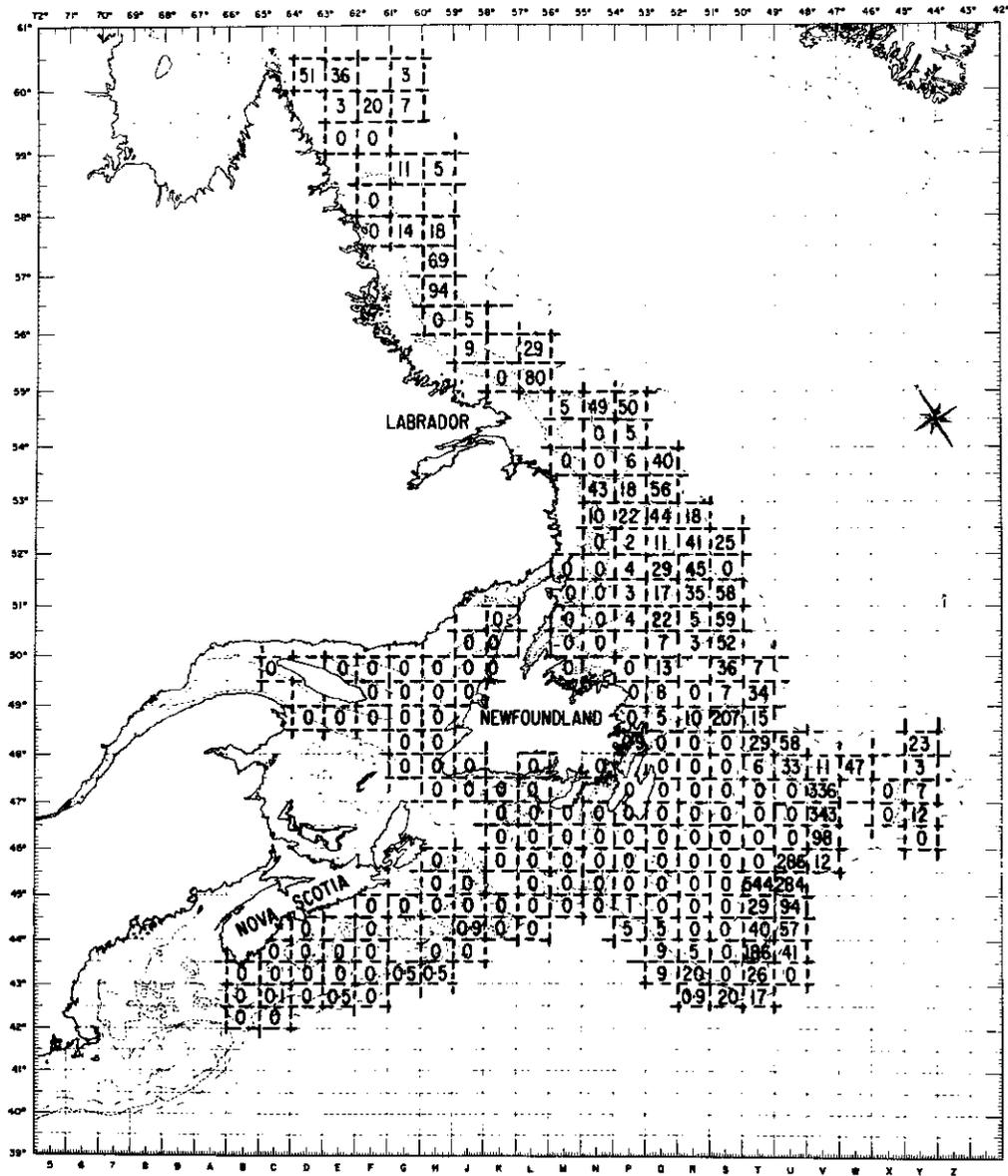


Fig. 5. Average catch of roughhead grenadier, kg whole weight, by 1/2 degree latitude, 1 degree longitude rectangle per 30-minute on bottom otter-trawling set of the A.T. Cameron during 1958-73.



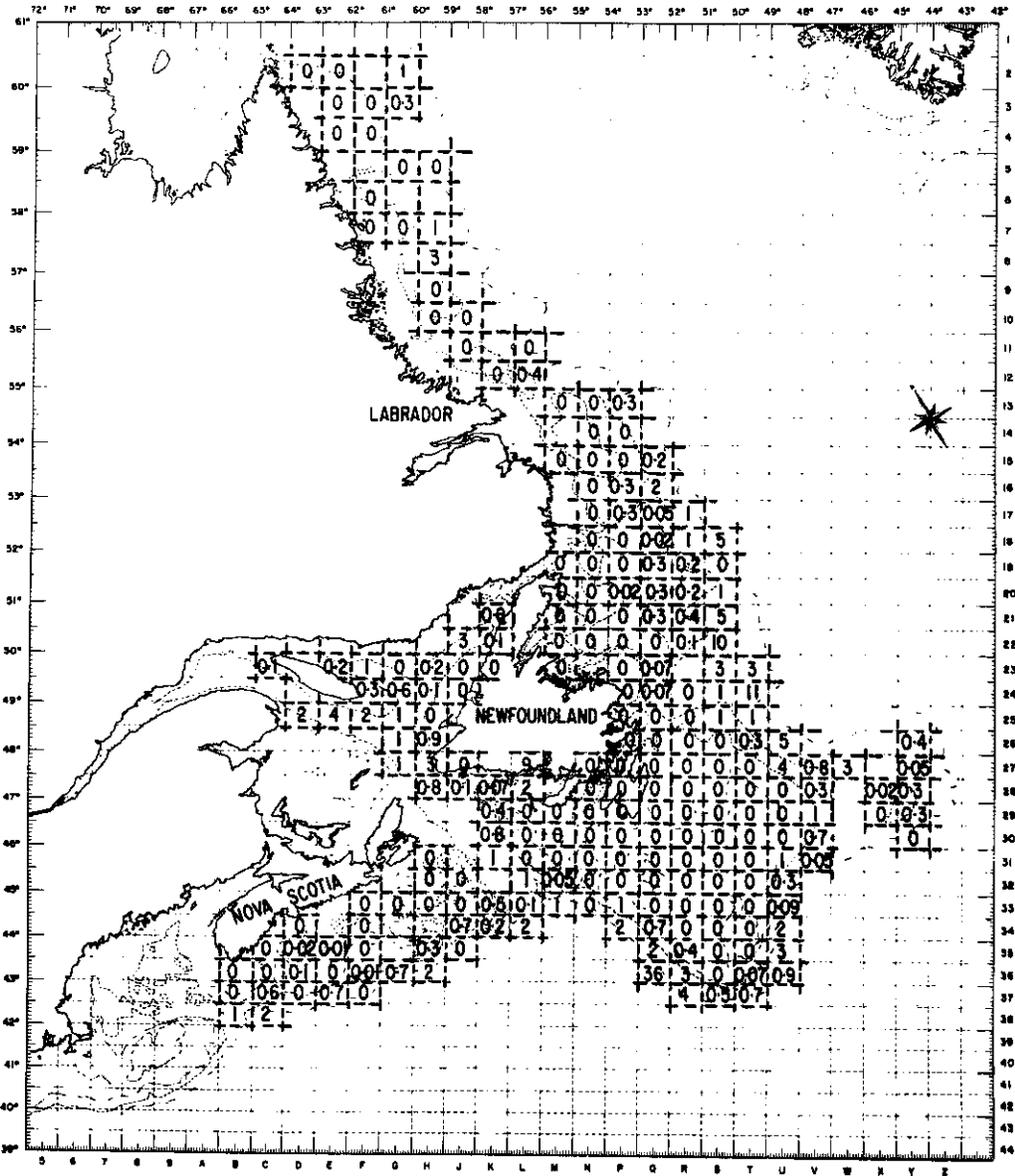


Fig. 7. Average catch of common grenadier, kg whole weight, by 1/2 degree latitude, 1 degree longitude rectangle per 30-minute on bottom otter-trawling set of the A.T. Cameron during 1958-73.

DISTRIBUTION BY DEPTH AND TEMPERATURE

Roundnose grenadier

Very few roundnose grenadiers were caught at depths less than 200 fm (366 m). In the area of greatest abundance (Div. 2G to 3K), the largest catches were generally obtained at depths greater than 275 fm (503 m). Similarly, very few roundnose grenadiers were caught at bottom temperatures of less than 3.5°C. The temperature range in areas where they were encountered in quantity was very narrow - generally 3.5 to 4.5°C. However, the species was taken in only very small quantities in deep water on the seaward slopes of the Grand Bank and Flemish Cap at bottom temperatures of 3.1 to 4°C and generally absent on the seaward slopes of St. Pierre Bank and the Scotian Shelf and in the Gulf of St. Lawrence where average bottom temperatures at depths greater than 200 fm (366 m) were slightly higher - 4.2 to 5.2°C.

Roughhead grenadier

Roughhead grenadiers were caught at depths as shallow as 100 fm (183 m) to the greatest depths fished (Table 2). Off northern Labrador (Div. 2H) greatest catches (>15 kg per 30-minute tow) were obtained at depths of 100 to 250 fm (183 to 457 m); in Div. 2J and 3K catches of approximately similar magnitude (10-20 kg) were taken at depths from 175 to 425 fm (320 to 775 m). In Div. 3L and 3N, the area of apparent greatest abundance of roughhead grenadiers, maximum catch rates were obtained at 175 to 275 fm (320 to 503 m) but there was very little difference in catch rates at depths from 150 to 400 fm (274 to 732 m). Roughhead grenadiers were caught in quantity (10 kg and more per tow) at average bottom temperatures as low as about 1.0°C and as high as 4.0°C but the greatest catches (in excess of 20 kg per tow) were generally obtained at bottom temperatures of 2.0 and 3.5°C.

Common grenadier

In the area from Div. 2H to 3L and 3M, common grenadiers were taken only infrequently at depths shallower than 200 fm (366 m) but they occurred somewhat shallower in the area from the southwestern Grand Bank to the Scotian Shelf with moderate quantities being taken as shallow as 125 fm (229 m) (Table 3). In almost all areas fished the species was caught at depths down to 425 fm (775 m). Greatest catches on the southwestern Grand Bank were obtained at depths of 275 to 425 fm (503 to 775 m). This species was generally taken at bottom temperatures ranging from 3.0 to 5.0°C, with greatest catches (>3 kg per tow) at temperatures of 3.0 to 4.0°C.

FISH SIZE BY DEPTH AND AREA

Roundnose grenadier

Average weights of roundnose grenadiers taken by otter trawl ranged from 0.04 to 1.7 kg (Table 4). In the areas of greatest abundance (Div. 2G and 3K) there was no apparent relationship between average weight of fish caught and depth. In Div. 3K the largest fish (0.9 to 1.7 kg) were caught at the shallower depths (150 to 250 fm; 274 to 457 m) and the smallest fish (0.2 to 0.4 kg) in deeper water (350 to 425 fm; 640 to 775 m). There were considerable area differences in average weight of fish caught with relatively small fish being taken in Div. 3L, 3M, 3N and 3O where average weights, with one exception, were less than 0.2 kg.

Roughhead grenadier

Average weights of roughhead grenadiers taken by otter trawl ranged from 0.1 to 2.3 kg but were generally between 0.5 and 1.1 kg (Table 5). In Div. 3N, the area of greatest abundance, the larger fish were shallower than the smaller fish. At depths less than 250 fm (457 m) the average weight of fish caught was in excess of 1.0 kg with the largest fish (1.4 to 1.9 kg) at depths of less than 125 fm (229 m). At depths greater than 250 fm (457 m) the average weight was less than 1.0 kg with relatively small fish (0.5 to 0.7 kg) taken at depths greater than 300 fm (549 m).

Common grenadier

The common grenadiers caught were small, with average weights generally ranging from 0.04 to 0.2 kg (Table 6). There was an apparent geographic size difference. Off Labrador and Northeast Newfoundland, the average weight of fish caught was around 0.2 kg, whereas on the eastern Grand Bank and Flemish Cap it was generally 0.1 kg; from the southwestern Grand Bank west to the Gulf of St. Lawrence and south to the Scotian Shelf it was generally less than 0.1 kg, with the smallest fish (about 0.05 kg), on the average, being taken on the Scotian Shelf (Div. 4VWX).

DISCUSSION AND CONCLUSIONS

Distribution

Roundnose grenadier. The roundnose grenadier occurs on both sides of the Atlantic and has been taken at depths down to 1,200 fm (2,200 m). It is distributed from about 37°N to Baffin Island and is also found off Greenland, Iceland and the Murman coast south to the Skaggeak and Irish Sea (Savvatimskii, 1969). Research catches reported here indicate that the centre of abundance in the Canadian area of the Northwest Atlantic occurs off northeast Newfoundland and Labrador. This species is restricted to deep water at the edge of the continental shelf at depths greater than 200 fm (366 m). Largest research

Table 3. Average weight (kg) of common grenadier catches per successful 30-minute trawl set in relation to depth and bottom temperature by ICMAF divisions (26 to 4X), based on A. T. *Camexon* catches during 1958-73 (number of sets in parentheses).

Depth (fm)	Area 0 Catch °C	Subarea 1 Catch °C	Div. 2G Catch °C	Div. 2H Catch °C	Div. 2J Catch °C	Div. 3K Catch °C	Div. 3L Catch °C	Div. 3M Catch °C	Div. 3M Catch °C	Div. 3N Catch °C	Div. 3O Catch °C	Div. 3P Catch °C	Div. 4RST Catch °C	Div. 4VWX Catch °C
0-25		0 (2) 4.9					0 (127) 0.1			0 (36) 2.5		0 (14) 1.7		0 (2) 6.3
26-50		0 (1) 1.7			0 (1) -0.2	0 (3) -0.4	0 (120) -0.5			0 (362) 1.2		0 (74) 1.0		0 (21) 0.9
51-75		0 (2) -0.3	0 (1) -0.3	0 (3) 0.8	0 (17) 0.8	0 (9) -0.4	0 (120) 0.0			0 (88) 0.6		0 (72) 3.7		0 (13) 3.4
76-100		0 (1) 2.4	0 (5) 0.4	0 (11) 0.7	0 (35) 1.7	0 (24) 1.3	0 (74) 0.9	0 (11) 3.8		0 (66) 0.9		0 (80) 4.4		0 (40) 4.3
101-125	0 (2) -0.9	0 (1) 3.0	0 (5) 2.0	0 (7) 0.5	0 (51) 2.6	0 (37) 2.1	0 (33) 1.4	0 (12) 4.2		0 (73) 1.5		0 (72) 2.6		0 (37) 5.2
126-150	0 (1) -1.1	0 (2) 0.8	0 (6) 3.5	0 (4) 1.2	0 (39) 3.3	0 (55) 3.0	0 (33) 2.3	0 (64) 4.2		0 (40) 1.8		0 (60) 4.3		0 (23) 6.0
151-175	0 (5) 0.7	0 (1) 3.9	0 (1) 3.9	0 (5) 2.2	0 (23) 3.6	0 (27) 3.1	0 (19) 3.3	0 (8) 4.0		0 (32) 2.2		0 (27) 3.9		0 (18) 5.5
176-200	0 (5) 1.3	0 (2) 3.2	0 (2) 3.9	0 (2) 2.0	0 (10) 3.6	0 (13) 3.3	0 (3) 3.4	0 (4) 3.9		0 (14) 2.7		0 (9) 3.8		0 (10) 5.7
201-225	0 (2) 2.4	0 (1) -	0 (1) 4.0	0 (1) 4.3	0 (11) 3.9	0 (14) 3.7	0 (9) 3.5	0 (5) 3.8		0 (3) 2.9		0 (3) 3.4		0 (4) 5.2
226-250	0 (1) 1.8	0 (3) 2.3	0 (1) 4.0	0 (3) 3.5	0 (4) 3.9	0 (9) 3.4	0 (4) 3.4	0 (4) 3.9		0 (6) 3.2		0 (4) 3.8		0 (9) 4.6
251-275	0 (1) 3.9	0 (1) 3.8	0 (1) 4.1	0 (1) 4.4	0 (8) 3.8	0 (8) 3.8	0 (6) 3.7	0 (25) 3.9		0 (2) 3.5		0 (5) 3.4		0 (4) 4.4
276-300	0 (1) 4.1	0 (1) 1.0	0 (1) 4.1	0 (2) 4.4	0 (7) 3.8	0 (6) 4.0	0 (2) 2.8	0 (7) 3.8		0 (2) 3.4		0 (6) 3.7		0 (5) 4.4
301-325	0 (1) 1.0				0 (5) 3.7	0 (6) 3.8	0 (3) 3.7	0 (4) 3.7		0 (4) 3.7		0 (2) 3.8		0 (1) 4.5
326-350		0 (2) 0.9			0 (1) 4.0	0 (3) 3.9	0 (3) 3.1	0 (5) 3.7		0 (1) 3.4		0 (2) 3.7		0 (2) 4.3
351-375	0 (3) 3.0	0 (1) 3.5	0 (1) 4.1	0 (1) 3.5	0 (4) 4.0	0 (3) 3.7	0 (3) 3.1	0 (5) 3.7		0 (4) 3.6		0 (4) 3.9		0 (1) 4.3
376-400		0 (1) 3.4	0 (1) 4.1	0 (1) 4.3	0 (3) 3.9	0 (4) 3.5	0 (1) 3.6	0 (3) 3.5		0 (1) 3.5		0 (2) 4.1		0 (1) 4.3
401-425					0 (1) 3.7					0 (1) 3.8				
426-450														
451-475														
476-500														0 (1) -

Table 4. Average weight (kg per fish) of roundnose grenadier taken by A.T. *Camexon*, 1958-73, in a No. 41-5 otter trawl on bottom at various depths (number of fish included in averages in parentheses).

Depth (fm)	Area 0 Aug-Sep	Subarea 1 Aug	Div. 2G Sep	Div. 2H Jul-Aug	Div. 2J Apr-Oct	Div. 3K Mar-Dec	Div. 3L May-Oct	Div. 3M Sep	Div. 3N Jul-Nov	Div. 3O May	Div. 4W Nov
151-175						0.9 (1)					
176-200						0.9 (5)				0.2 (15)	
201-225							0.9 (47)			0.1 (70)	
226-250			0.8 (2500)		0.6 (7)	0.5 (537)	0.1 (3)			0.1 (45)	
251-275					0.6 (4)	0.5 (13)				0.1 (80)	
276-300	0.9 (32)	0.6 (14)			0.5 (6024)	0.7 (1099)		0.05 (5)	0.08 (54)	0.2 (175)	
301-325	1.4 (1)	0.6 (32)		0.6 (47)	0.5 (22)	0.7 (1099)				0.2 (60)	
326-350					0.6 (19)	0.8 (2071)			0.1 (129)	0.2 (60)	
351-375						0.2 (582)			0.4 (202)	0.1 (360)	
376-400	0.2 (1046)	0.5 (438)		0.6 (304)	0.3 (194)	0.4 (1910)				0.1 (276)	
401-425		0.6 (4185)			0.8 (75)	0.3 (443)					

Table 5. Average weight (kg per fish) of roughhead grenadier taken by A.T. Camezov, 1958-73, in a No. 41-5 Otter trawl on bottom at various depths (number of fish included in average, in parentheses).

Depth (fm)	Area 0 Aug-Sep	Subarea 1 Aug	Div. 26 Sep-Oct	Div. 2H Jul-Oct	Div. 2J Apr-Nov	Div. 3K Feb-Dec	Div. 3L Feb-Nov	Div. 3M Mar-Sep	Div. 3N Feb-Nov	Div. 30 Feb-Dec	Div. 4VWX Nov
26-50											
51-75				0.5 (1)					1.4 (5)		
76-100			1.4 (4)	0.5 (7)					1.6 (59)		
101-125			1.3 (24)	1.0 (127)	0.8 (29)	0.8 (3)	0.8 (6)		1.9 (432)	0.6 (2)	
126-150			0.6 (25)	0.9 (155)	1.0 (133)	0.8 (45)	1.0 (59)		1.6 (886)	0.9 (15)	
151-175			0.6 (10)	1.2 (127)	0.8 (111)	0.8 (166)	0.7 (904)		0.7 (262)	0.8 (66)	
176-200				0.8 (152)	0.7 (75)	0.8 (216)	1.0 (504)	0.9 (1)	1.2 (344)	0.9 (35)	
201-225		0.4 (65)	0.5 (14)		0.9 (126)	1.0 (129)	0.8 (110)	0.6 (25)	1.0 (151)	0.8 (22)	
226-250			0.7 (4)	0.5 (98)	0.6 (124)	0.6 (196)	0.9 (342)	1.0 (40)	1.0 (53)	0.5 (23)	
251-275		0.2 (6)			0.6 (32)	0.8 (113)	0.8 (114)	1.1 (38)	1.1 (173)	0.3 (12)	
276-300		0.7 (61)	0.5 (9)		0.6 (107)	0.7 (100)	0.6 (181)	0.7 (166)	0.9 (61)	0.9 (19)	
301-325		1.4 (16)	2.3 (3)	0.4 (37)	0.5 (26)	0.7 (72)	1.0 (14)	1.1 (117)	0.9 (176)	1.2 (29)	0.2 (2)
326-350					0.9 (74)	0.9 (102)	0.5 (57)	0.9 (52)	0.7 (36)		
351-375		0.5 (1)				0.7 (75)	0.7 (141)		0.6 (169)	0.6 (11)	
376-400	0.5 (47)	0.4 (10)	0.5 (29)	0.3 (14)	0.7 (101)	1.1 (75)	0.6 (26)	1.1 (58)	0.5 (16)	0.7 (27)	0.5 (2)
401-425		0.8 (23)		0.5 (13)	0.8 (45)	0.6 (94)		1.0 (54)	0.7 (142)	1.0 (14)	0.1 (1)
426-450									0.6 (4)		

Table 6. Average weight (kg per fish) of common grenadier taken by A.T. Camezov, 1958-73, in a No. 41-5 otter trawl on bottom at various depths (number of fish included in average, in parentheses).

Depth (fm)	Area 0 Aug-Sep	Div. 2H Jul-Aug	Div. 2J Apr-Oct	Div. 3K Feb-Dec	Div. 3L Mar-Nov	Div. 3M Mar-Sep	Div. 3N Feb-Nov	Div. 30 Feb-Dec	Div. 3P Jan-Dec	Div. 4RST Jan-Nov	Div. 4VWX May-Dec
26-50											
51-75								0.05 (1)			0.05 (15)
76-100											
101-125							0.1 (2)	0.05 (40)	0.1 (12)	0.09 (14)	0.05 (1)
126-150			0.2 (1)				0.1 (15)	0.06 (480)	0.07 (443)	0.1 (109)	0.04 (51)
151-175		0.2 (9)	0.6 (4)				0.3 (47)	0.07 (1242)	0.06 (1170)	0.09 (689)	0.08 (82)
176-200			0.2 (5)				0.08 (118)	0.09 (535)	0.09 (552)	0.08 (657)	0.06 (83)
201-225			0.2 (9)				0.09 (162)	0.1 (215)	0.09 (186)	0.08 (1095)	0.07 (24)
226-250		0.2 (67)	0.2 (104)				0.2 (52)	0.1 (90)	0.09 (186)	0.08 (40)	0.08 (20)
251-275	0.2 (2)		0.2 (27)				0.1 (12)	0.1 (131)	0.07 (221)	0.09 (98)	0.07 (75)
276-300		0.2 (6)	0.2 (96)				0.1 (77)	0.08 (230)	0.09 (210)	0.08 (179)	0.08 (33)
301-325			0.2 (21)				0.1 (869)	0.2 (180)			0.06 (53)
326-350			0.2 (70)				0.1 (63)				0.06 (62)
351-375							0.2 (150)	0.2 (550)			0.04 (43)
376-400											0.05 (131)
401-425		0.5 (1)	0.2 (2)				0.1 (224)	0.2 (395)			0.07 (42)
			0.2 (11)				0.2 (59)	0.2 (500)			

catches were obtained at depths greater than 275 fm (503 m). This species was not taken in quantity at bottom temperatures less than 3.5°C.

USSR investigations have shown that the roundnose occurs in commercial concentrations on the edge of the northeast Newfoundland Shelf at depths from 250 to 550 fm (457 to 1,006 m) and deeper (Savvatimskii, 1969; Pechenik and Troyanovskii, 1970). According to Savvatimskii (1971), at present only feeding concentrations of immature grenadiers are exploited, these being found at shallower depths than the adult fish. Stanek (1971) reports that the roundnose or rock grenadier is the dominant species in commercial grenadier catches, with yields at the inception of commercial exploitation of up to 10 tons per hour of trawling. The proportion of roundnose grenadier in the catches increases with depth; at a depth of 800 m it is the only grenadier species caught (Stanek, 1971). ICNAF statistics since 1967 indicate that, with the exception of 1971, more than 80% of the roundnose grenadier catch has been taken in Div. 3K. In 1971, 72% of the catch was taken in Div. 2G. Our catch records suggest that the greatest concentrations of roundnose grenadier occur during the second half of the year, but we have not fished this area to any great extent during the January-March period. An examination of monthly commercial catch records for Div. 3K during 1972-73 shows that 83% of the catches were taken during the June-October period. According to Savvatimskii (1969), the roundnose grenadier is encountered in commercial concentrations during the autumn.

Farther to the south, exploratory deep-sea otter trawling by the Woods Hole Oceanographic Institution vessel *Caryn* in 1952 and 1953 yielded catches of 220 to 535 roundnose grenadiers per haul (one-half to one hour duration) at depths of 300 to 550 fm (549 to 1,006 m) off the southeastern edge of the Nova Scotian Shelf, extending from longitude 63°16'W to 65°39'W (Schroeder, 1955). The shoalest capture of this species was in the 201 to 250 fm (386 to 457 m) zone and the deepest around 700 fm (1,280 m). Markle and Musick (1974) report the capture of *Coryphaenoides rupestris* at depths of 800-950 m in the middle Atlantic Bight (approximately 39°30' to 39°50'N) but *Nezumia* spp. (particularly *Nezumia bairdii*) were the dominant grenadiers in terms of numbers.

Roughhead grenadier. The roughhead grenadier has been reported to occur in deep water on both sides of the North Atlantic, along the continental slope of North America south to Georges Bank, in Davis Strait, off southern Greenland, Iceland, Spitzbergen and northern Norway (Savvatimskii, 1969). Research surveys indicate that this species is more widely dispersed than the roundnose and, although also a deep-water species, occurs in greatest numbers at somewhat shallower depths (100 to 275 fm; 183 to 503 m) than the roundnose. Largest catches of roughhead grenadiers were taken during July to September along the eastern and northern edge of the Grand Bank (Div. 3L and 3N), but even there average catch rates were considerably less than the average catches of roundnose grenadier obtained in their area of greatest abundance off northeast Newfoundland and Labrador. Greatest catches of roughheads have been generally taken at bottom temperatures between 2.0 and 3.5°C, as contrasted with roundnose grenadiers, very few of which were caught at bottom temperatures of less than 3.5°C. Marshall and Iwamoto (1973), citing Andriashev (1964) note that *Macrourus berglax* is more of a cold water form than *Coryphaenoides rupestris* occurring in the Norwegian and Barents seas at temperatures close to 0°C, but has yet to be found in waters below 0°C.

Common grenadier. Greatest catches of this species were obtained on the southwestern edge of the Grand Bank at bottom temperatures of 3.0 and 4.0°C. Unlike the roundnose and roughhead, it is present in the Gulf of St. Lawrence. Average catches per set have been very small in comparison with those for the other two species.

Size, age, food and migrations

Because relatively little is known of the biology and life history of the roughhead and common grenadiers, the following comments pertain only to the roundnose.

The commercial fishery for roundnose grenadier off northeast Newfoundland-Labrador has been reported to be based on 9- to 14-year-old fish, 60-70 cm in length and 0.36 to 0.75 kg in weight (Savvatimskii, 1972). The females grow somewhat more rapidly than the males. The roundnose is apparently long-lived and attains sexual maturity relatively late. The fishery in the Northwest Atlantic is based on feeding concentrations of sexually immature fish. The roundnose grenadier is primarily a bathypelagic feeder, as contrasted with the roughhead grenadier which is primarily a bottom feeder (Konstantinov and Pondrazhanskaya, 1972). Euphausiids and copepods, squid and such fish species as lanternfish and redfish are prominent in the diet of the roundnose, but polychaetes, *Ophiura* and crabs dominate in the diet of the roughhead.

Knowledge of stock relationships and migrations of the roundnose grenadier is scanty.

USSR scientists have proposed conflicting hypotheses on the extent of migrations exhibited by the roundnose. Zakharov and Mokuau (1970) suggested that the roundnose grenadier spawns in Iceland waters, the eggs and larvae are transported passively by the currents around West Greenland to Baffin Island and thence by the Labrador Current to the Northeast Newfoundland Shelf where the young settle to bottom at depths of 330 to 500 fm (603 to 914 m); as the fish grow larger, they migrate back to the Icelandic spawning areas. More recently, this hypothesis has been discounted by Savvatimskii (1972), who, from a consideration of external body structure, considers the roundnose grenadier to be a poor swimmer. It appears more likely that concentrations of sexually mature grenadiers in the Northwest Atlantic occur at depths greater than those normally fished commercially. This has been confirmed by capture during exploratory fishing of large sexually mature fish at depths of about 1,470-1,520 m off central Labrador and of spawning and post-spawning fish at depths of 850 to 1,270 m off Nova Scotia (Savvatimskii, 1972). The percentage of mature fish increases with depth.

Information about time of spawning is very sparse. It has been suggested (Grigorev, 1972) that spawning is non-intermittent and occurs year round. According to Grigorev (1972), juvenile roundnose grenadiers, approximately 8 cm long, are encountered along the continental slope of North America from the Grand Bank to Cumberland Peninsula, also along West Greenland and south of Iceland. In research catches by the A.T. Cameron, roundnose grenadiers taken in Div. 3L, 3M, 3N and 3O generally had average weights of less than 0.2 kg and, in some instances, as little as 0.04 to 0.05 kg. It seems reasonable to assume that juveniles caught on the continental slope off Newfoundland, Labrador and West Greenland have a local origin with spawning occurring in these regions at depths greater than 1,000 m - at the bottom or in the bathypelagic zone. Marshall and Iwamoto (1973) suggest that both *Coryphaenoides rupestris* and *Nezumia bairdii* are summer-autumn spawners.

Marshall (1965) suggests that the movements of grenadiers along the continental slope do not exceed a hundred miles, while such movements are even less across the continental slope.

There is evidence that the roundnose grenadier, a bathypelagic feeder, undertakes diurnal vertical migrations (Savvatimskii, 1969). Haedrich (1974) reports the capture of 49 specimens of *Coryphaenoides rupestris* (7-94 cm in length) during midwater trawling by the German research vessel *Walther Herwig* off Iceland. These specimens were caught in seven midwater hauls, both day and night, 270-1,440 m off the bottom at depths between 1,000 and 2,100 m. Modal distance off the bottom was about 480 m. Haedrich (1974) concluded from these captures, and recent studies showing that *Coryphaenoides* feed largely on pelagic animals, that slope dwelling members of this genus normally move off the bottom and feed in midwater.

Resource potential

Fishes of the family *Macrouridae* are dominant, both in biomass and numbers, on the continental slopes and abyssal plains of many regions of the world (Grey, 1956; Marshall, 1965; Kort, 1967; Iwamoto, 1970; Percy and Ambler, 1974). In all, about 300 species of grenadiers have been described, of which approximately 65 species occur in the Atlantic (Marshall and Iwamoto, 1973), half of which occur in the Gulf of Mexico and the Caribbean Sea. Only the three species discussed here are commonly taken in trawl catches on the continental slopes off the Canadian Atlantic coast.

Only the roundnose grenadier has been caught in commercial quantities with catches of this species reported separately to ICNAF since 1967. Catches fluctuated between 13,000 and 32,000 tons from 1967 to 1973, except for 1971 when 75,000 tons were caught (Fig. 8). Estimates of 24,000 and 37,000 tons have been recently derived as preliminary lower and upper limits of maximum sustainable yield for roundnose grenadiers in ICNAF Subareas 2 and 3 (Pinhorn, MS 1974). To date, the fishery has apparently only exploited concentrations of immature fish and these are apparently fully exploited at the present time. However, these estimates of maximum sustainable yield probably represent the potential of only the immature portion of the stock. The potential of the total stock may be substantially higher if the fishery were extended to mature fish at greater depths.

The roughhead grenadier probably occurs in limited numbers in commercial grenadier catches off northeast Newfoundland and Labrador but the proportion of roughheads in these grenadier catches is probably small. From its depth distribution, which overlaps that of redfish, it appears likely that roughheads are taken frequently as a by-catch in the redfish fishery in Div. 3L to 3N.

Because of its limited biomass and small size (generally 0.1-0.2 kg) the common grenadier is unsuitable for commercial exploitation.

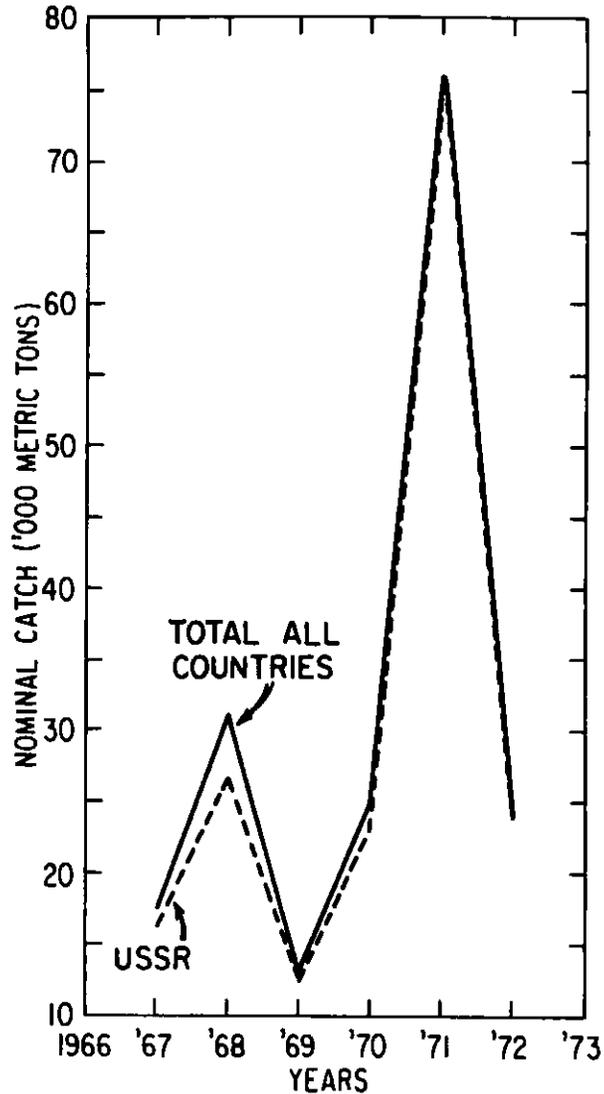


Fig. 8. Nominal catches of roundnose grenadiers from ICNAF Subareas 2 and 3.
Note: Catches of this species were first recorded in ICNAF statistics for 1967 although quantities were probably taken before then and included under unspecified groundfish.

Moiseev (1973) gives the 1970 world catch of Macrurids as about 300,000 tons and estimates a worldwide potential catch of about one million tons, a large proportion of this from the southern hemisphere, Suda (1973) estimates the potential catch of Macrurids and morids in the northern hemisphere as about 150,000 tons. Gulland (1970) estimates a potential catch of 100,000 tons of macrurids from the Northeast Pacific.

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An Overview of the Plankton Communities of the Gulf of Maine¹

by

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ABSTRACT

The standing stock of phytoplankton in the Gulf of Maine is characterized by a winter minimum, a heavy spring bloom, a sharp decrease during the summer almost to winter levels, and a moderate autumn bloom followed by a decline in biomass to the winter minimum values. The seasonal changes in primary productivity are similar to those in biomass, except that the summer decline does not appear to be as severe. The annual primary production in the Gulf of Maine is in the range of 100-200 g C/m²/year.

The zooplankton of the Gulf of Maine has been characterized as a *Calanus* community. The most abundant species in the Gulf are *Calanus finmarchicus*, *Pseudocalanus minutus* and *Metridia lucens*. Oceanic species and the larvae of benthic organisms are abundant at various times during the year. The abundance and distribution of zooplankton seems to be greatly influenced by variations in the large scale circulation of the Gulf of Maine and Georges Bank as well as by smaller scale phenomena.

INTRODUCTION

This paper was written in response to the request by the ICNAF Environmental Working Group for an overview of the biological system of the Gulf of Maine. It summarizes the knowledge of the phytoplankton and zooplankton, including a description of dominant species as well as biomass and productivity data for these components in the Gulf of Maine. The paper does not cover planktonic bacteria, fungi, or protozoans nor does it include the benthos or fishes, but rather it gives a synopsis of the phytoplankton and zooplankton communities as a basis for an understanding of the biological system in the Gulf of Maine, particularly with reference to factors controlling survival of larval fish.

Only a generalized view of the plankton communities in the Gulf of Maine is possible because the few broad scale studies that have been conducted were carried out at different times using disparate methods and some of them were qualitative in nature. This is particularly true in the case of production and biomass estimates, where much of the early data is more qualitative than quantitative. Nevertheless, increased knowledge about the lower trophic levels is fundamental to better understanding of fish production, and even qualitative studies will point out areas where additional research is necessary.

The area covered in this paper is shown in Fig. 1. The Gulf of Maine includes the oceanic bight from Nantucket in the west to Cape Sable in the east, including Nantucket Shoals, Georges Bank and Browns Bank, extending out to the 200-meter depth contour. The flora and fauna of the Gulf of Maine is primarily a boreal assemblage of species, with subtropical, tropical, temperate and arctic immigrants at various times of the year. The general non-tidal surface circulation in the deep basin of the Gulf of Maine consists of a counter-clockwise gyre most of the year, with a clockwise gyre on Georges Bank in the spring and summer (Bumpus, 1973). The bottom circulation in the Gulf and on Georges Bank appears to be in the same direction as the surface flow but at lower velocities.

This paper is divided into two major sections, in which phytoplankton and zooplankton are dealt with separately. The phytoplankton section contains information on the seasonal and geographic changes in species composition, standing stock and primary production, as well as material on the factors limiting phytoplankton growth in the Gulf of Maine. The zooplankton section contains a synopsis of the reproductive cycles of dominant species and of variations of biomass and abundance of zooplankton throughout the year.

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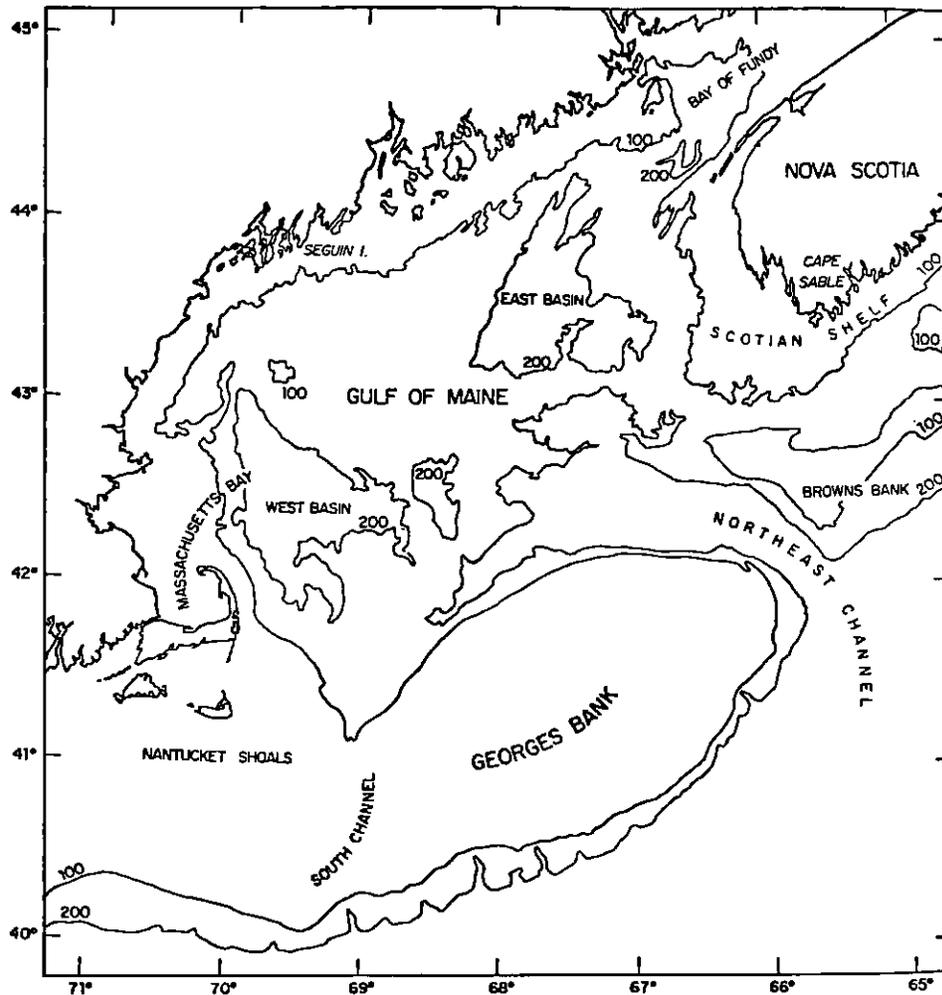


Fig. 1. The Gulf of Maine (depths in meters).

PHYTOPLANKTON

Phytoplankton studies in the Gulf of Maine were carried out as early as 1912 (Bigelow, 1914). Further work by Bigelow resulted in his classic work on the plankton of the off-shore waters of the Gulf of Maine (1926). These studies employed plankton nets and therefore present only a qualitative picture of the larger phytoplankton. Yentsch and Ryther (1959) found that phytoplankton nets do not sample the nannoplankton (those phytoplankton that will pass through the pores of a fine plankton net) and that the abundance of larger forms may also be underestimated due to clogging. Studies carried out by Gran and Braarud (1935), Bigelow, Lillick and Sears (1940), Lillick (1940), Sears (1941), Riley (1941, 1946), and Hulburt and Corwin (1970) provide a more quantitative picture of the phytoplankton community in the Gulf of Maine. With the exception of the study by Hulburt and Corwin (1970) all of the studies mentioned above were carried out in the early 1930's. Although the seasonal phytoplankton cycle based on those studies is presented in this paper in a generalized manner, it should be noted that a complete time series of sampling throughout the year does not exist.

Dominant species

The dominant phytoplankton of the Gulf of Maine are the diatoms, with approximately 130 species present in the plankton during the course of a year. The diatoms are followed in importance by the dinoflagellates and coccolithophorids. Silicoflagellates are often widespread in the Gulf of Maine but rarely are they the dominant phytoplankton.

Another type, *Phaeocystis*, is never widespread but may be abundant locally. Lillick (1940) reported a bloom in Massachusetts Bay for a short period of time, but Parker and

Mulligan (TRIGOM-PARC,1974) found no *Phaeocystis* in their study of Massachusetts Bay in 1972-1973. There are large numbers of small green flagellated nanoplankton (called muflagellates by Lillick, 1940), which were otherwise unidentifiable but possibly of great importance in terms of their contribution to the annual primary production of the area. Yentsch and Ryther (1959) have observed that the nanoplankton in southern New England waters contribute about 92% of the total photosynthesis. This figure is in accord with values determined by Malone (1971) who found that the nanoplankton contributed about 90% on the average to primary production. The nanoplankton become relatively more important as the nutrient concentration decreases (Malone,1971) and so they can be expected to be particularly important during the summer months.

Seasonal and geographic variations in species composition

Most of the following discussion on species composition is based on the work of Lillick (1940). The species composition of the phytoplankton varies with the season and also geographically within a season (Fig. 2 to 7). The smallest number of species are present in the Gulf of Maine during the winter. At the time of the spring phytoplankton bloom, the number of species increases, remains at a fairly high level through the summer and early autumn, and then decreases in late autumn. The following discussion will pertain to the Gulf of Maine in general, unless an area within this region is specifically mentioned.

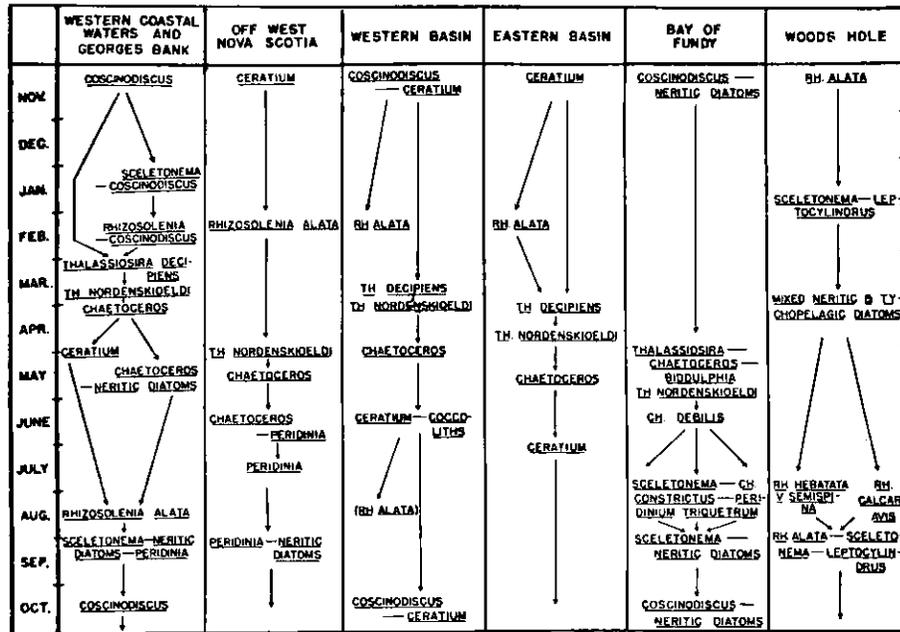


Fig. 2. Seasonal succession of dominants in representative parts of the Gulf of Maine (derived from all sources). From Lillick (1940).

Winter flora. The winter flora is characterized by a paucity of both species and individuals (Bigelow, Lillick and Sears, 1940; Lillick, 1940; Sears, 1941). Generally the dominant species at this time of year are *Chaetoceros excentricus*, *C. centralis*, *Thalassionema nitzschoides*, *Ceratium longipes*, *C. tripos* and *Prorocentrum micans* although the importance of the various species will vary from place to place within the Gulf (Fig. 2 and 3). For example, *Cosinodiscus* and *Ceratium* are the dominant forms in the western and northern coastal areas, while *Peridinium*, *Exuviella* and the neritic diatoms, *Melosira sulcata* and *Thalassionema nitzschoides*, are the most important on the eastern side of the Gulf. On Georges Bank there is still another assemblage of species: *Ceratium*, other dinoflagellates, *Cosinodiscus* and other neritic forms occur in about equal numbers.

In general, as the winter progresses, *Cosinodiscus* becomes the dominant phytoplankter in the Gulf of Maine, and boreal species which are rare at the beginning of winter, such as *Biddulphia*, *Chaetoceros*, *Rhizosolenia alata*, *Thalassenoma nitzschoides*, and *Skeletonema costatum* (in coastal areas) increase in numbers. It is at this time, too, that some

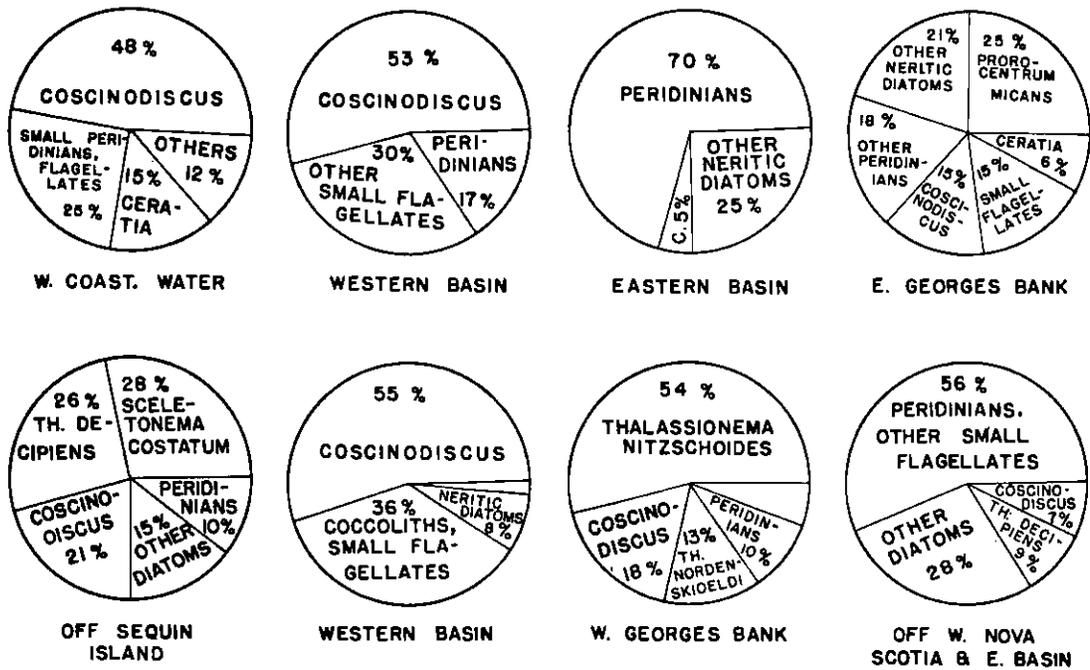


Fig. 3. Percentage composition of the phytoplankton at representative localities in the Gulf of Maine; above, December 1933 (C. = Coscinodiscus); below, January 1934. From Lillick (1940).

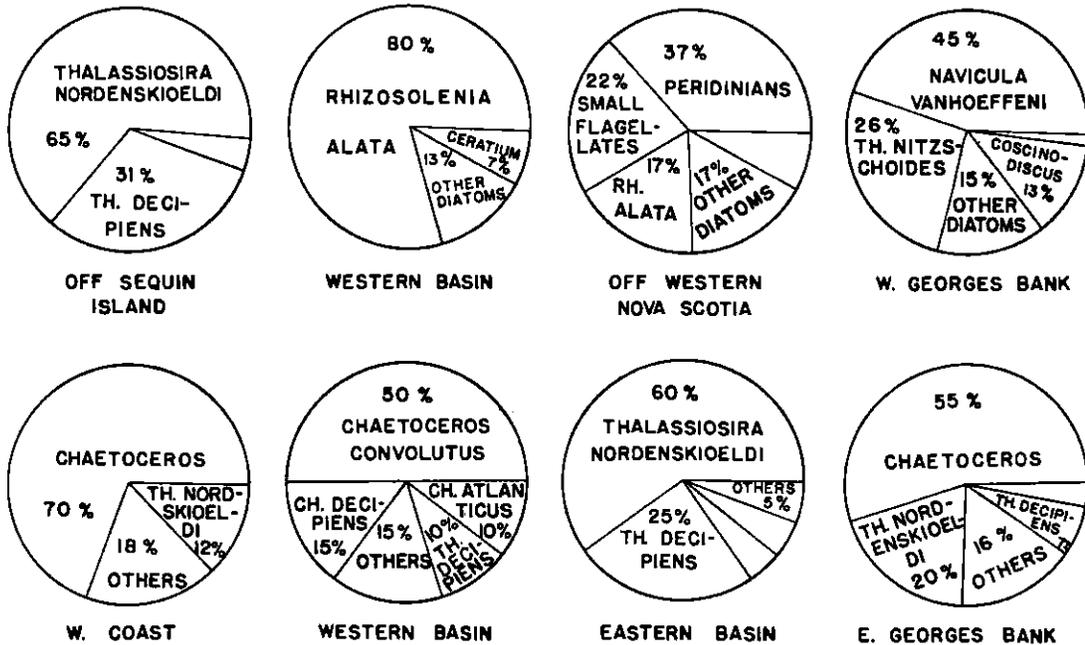


Fig. 4. Percentage composition of the phytoplankton at representative localities in the Gulf of Maine in 1934; -- March (above) and late April-early May (below). From Lillick (1940).

arctic forms appear (e.g. *Navicula van hoeffeni*) and that the dinoflagellates reach their nadir. The dinoflagellates are at a disadvantage at this time (and into the spring), because the lower temperatures mean an increased solubility of carbonate (Harvey, 1966).

Spring flora. The spring phytoplankton bloom starts sometime between early February and early April in the Gulf of Maine. The species composition at several places within the Gulf of Maine is given in Fig. 2 and 4. The first species to bloom in the major

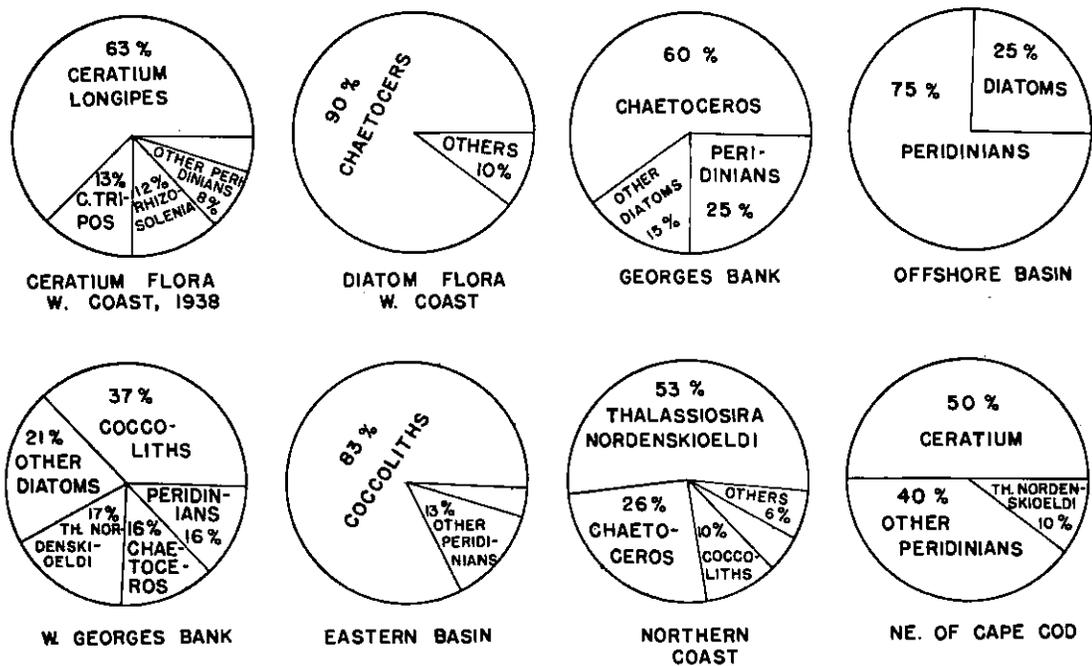


Fig. 5. Percentage composition of the phytoplankton at representative localities in the Gulf of Maine, late May-early June 1934 (above), and late June-early July 1933 and 1934 (below). From Lillick (1940).

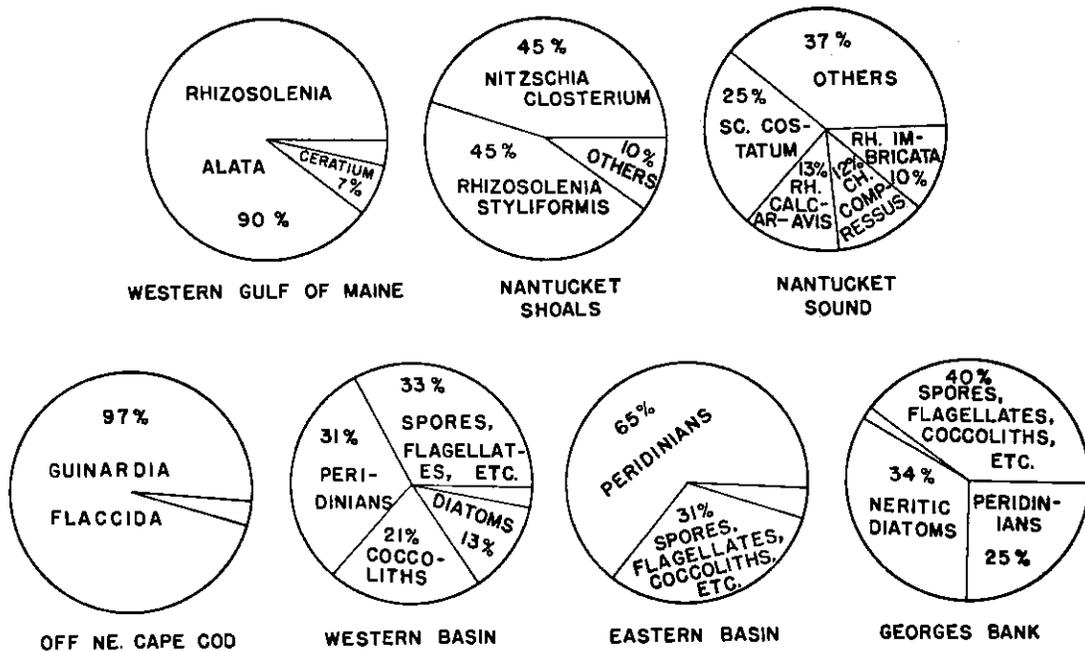


Fig. 6. Percentage composition of the phytoplankton at representative localities in the Gulf of Maine, August 1936 (above) and September 1933 (below). From Lillick (1940).

portion of the Gulf are *Thalassiosira decipiens* and *T. nordenskoeldi*, while *Chaetoceros socialis* initiates the bloom on Georges Bank (Lillick, 1940; Sears, 1941). The most abundant organism in the Gulf of Maine at this time is *T. nordenskoeldi* followed by *T. decipiens*, *T. gravida*, and *Porosira glacialis*. Other less abundant but important species are *Chaetoceros borealis*, *C. convolutus*, *C. debilis*, *C. decipiens*, *C. compressus*, *C. laciniosis*, *C. furcellitus*, some arctic forms, *Fragilaria oceanica*, *Navicula van hoeffeni*, *Achnanthes taeniata*, and a cold-water dinoflagellate *Ceratium arcticum* in the eastern Gulf of Maine. Although *Thalassiosira* is the usual dominant phytoplankton, *Chaetoceros debilis* and other species of *Chaetoceros* are sometimes the most abundant phytoplankton.

Summer and autumn flora. The species composition at various locations in the Gulf of Maine during the summer is represented in Fig. 2 and 5. By early summer the most important species in the Gulf of Maine will include the following diatoms: *Chaetoceros* sp., *Coscinodiscus centralis*, *Guinardia flaccida*, *Leptocylindrus danicus*, *Rhizosolenia*, *Thalassionema nitzschooides*, *Thalassiosira decipiens*, *T. nordenskoeldi* and *Thalassiothrix longissima*. However, in some years in the deep basin there will be virtually no diatoms in the early summer but instead a dinoflagellate community. This assemblage will include *Ceratium longipes* (maximum abundance in July), *Ceratium tripos* (maximum abundance in August), *C. bercephalum*, *C. fusus*, *Peridinium depressum*, *P. conecum*, *P. crassipes*, *Dinophysis* sp., *Exviella* sp., and occasionally *Coccolithus huxleyi*.

By midsummer in the deep basin of the Gulf, the dinoflagellates *Ceratium* and *Peridinium*, become the dominant forms even in years when the early summer flora consist predominantly of diatoms (Fig. 2 and 6). This may be due to the increased water temperature and the fact that some dinoflagellates can vertically migrate 10-20 m into nutrient rich waters below the thermocline (Epply et al., 1969). On Georges Bank the diatoms continue to dominate the phytoplankton, probably because the wind and tidal mixing of the water column ensure a supply of nutrients regenerated on the bottom. The species found on Georges Bank in the summer include *Chaetoceros* sp., *Rhizosolenia*, *Leptocylindrus minimus*, *Coccolithus huxleyi* and a small form of *Thalassiosira* (Sears, 1941).

The late summer flora (August-September) (Figures 2 and 7) is characterized by a second less intense diatom bloom in shoaler waters of the Gulf of Maine. In the coastal regions of the Gulf, *Chaetoceros debilis*, *C. decipiens*, *C. compressus*, *C. lacineosis*, *Skeletonema costatum* and *Rhizosolenia alata* are the most important species. On Georges

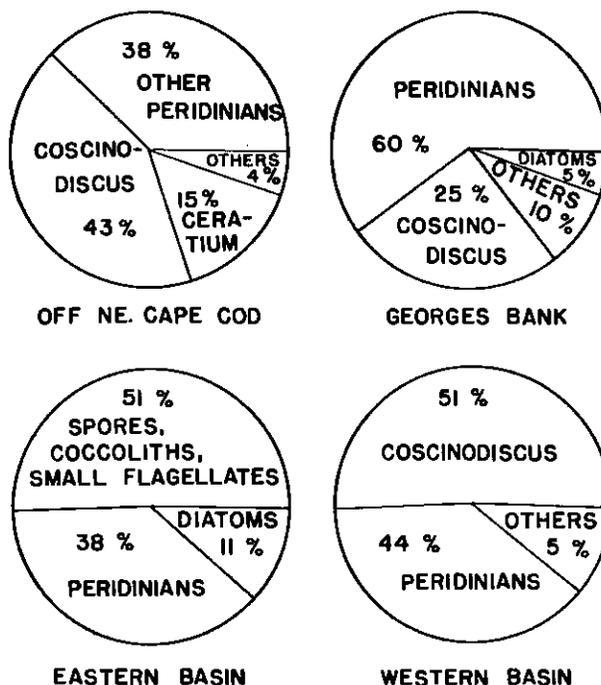


Fig. 7. Percentage composition of representative localities in the Gulf of Maine, October 1933. From Lillick (1940).

Bank *Rhizosolenia alata* is the most abundant species, although *R. setigera*, *R. imbricata* and *R. lebatata* are also important. The phytoplankton of the deep portions of the Gulf of Maine consists predominantly of dinoflagellates, although silicoflagellates are at their seasonal peak, and occasionally *Coccolithus huxleyi* will bloom. After the autumn bloom, a mixed flora of dinoflagellates and diatoms persists on Georges Bank (Sears, 1941) and in the coastal regions of the Gulf of Maine. The species present include *Guinardia flaccida*, *Thalassionema gravida*, *Coscinodiscus concinnus*, several species of *Chaetoceros*, *Rhizosolenia*, *Melosira sulcata*, and *Ceratium*, together with a large variety of neritic and tychopelagic diatoms. In the whole region, late September is the end of active growth of the phytoplankton and the beginning of the transition to the winter minimum, *Chaetoceros* dominated flora.

Seasonal cycles of biomass and primary productivity

The phytoplankton standing stock in the Gulf of Maine is characterized by a winter minimum, a heavy spring bloom, a sharp decrease during the summer almost to winter levels, and a moderate autumn bloom followed by a decline in standing stock to the winter minimum values (Fig. 8 and 9). The standing stock of phytoplankton on Georges Bank is much greater at all seasons of the year than in other parts of the Gulf of Maine. Primary productivity measurements are available only for Georges Bank and Massachusetts Bay. The seasonal changes in primary productivity are similar to those of the biomass except that following the spring bloom primary production does not decline as rapidly as the biomass.

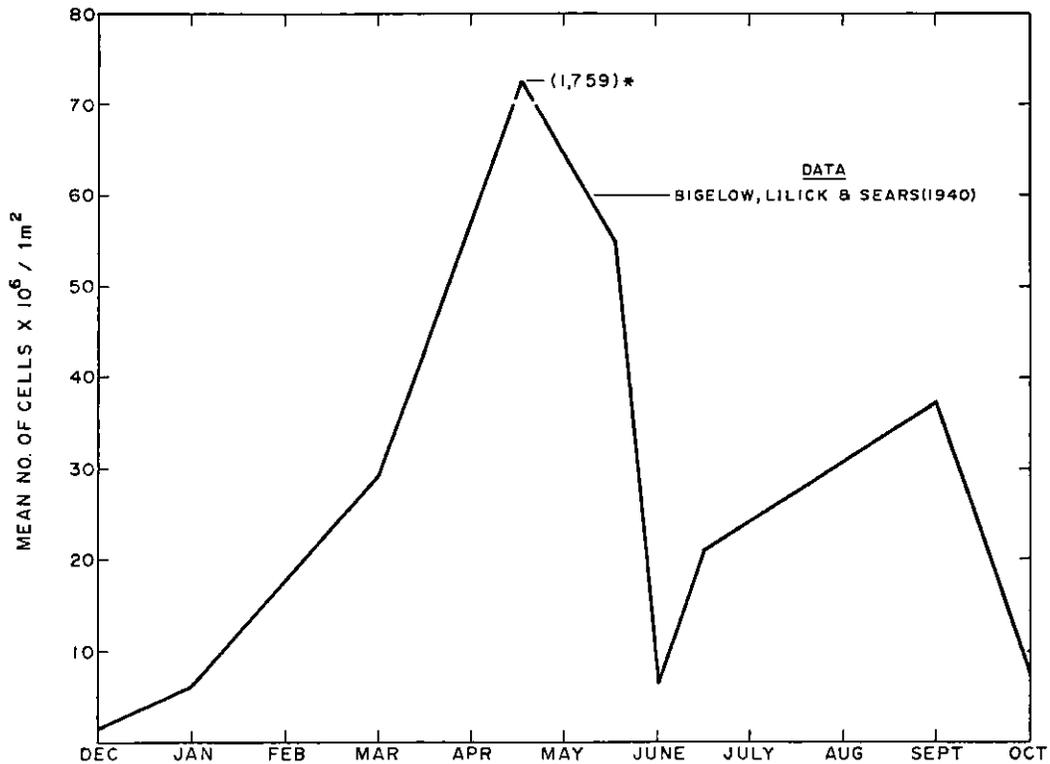


Fig. 8. Phytoplankton abundance in the Gulf of Maine. (* = value exceeds graph scale.)

The information on biomass and productivity summarized in Fig. 8 to 10 represents a composite of information given in Bigelow *et al.* (1940), Riley (1941), Sears (1941) and Parker and Mulligan (TRIGOM-PARC, 1974). The values for chlorophyll in Fig. 9 are derived from Riley's (1941) plant pigment analysis, which employed Harvey Plant Pigment Units (HPPU), using a conversion factor of mg chlorophyll = $(3 \pm 1 \times 10^{-4}) \times$ (No. of HPPUS) (Strickland, 1960). These rough estimates of the chlorophyll content/m² are subject to additional error, because the methods employed to concentrate the phytoplankton for pigment analysis did not adequately sample the nannoplankton; however, they should be adequate for an indication of gross changes in the standing stock.

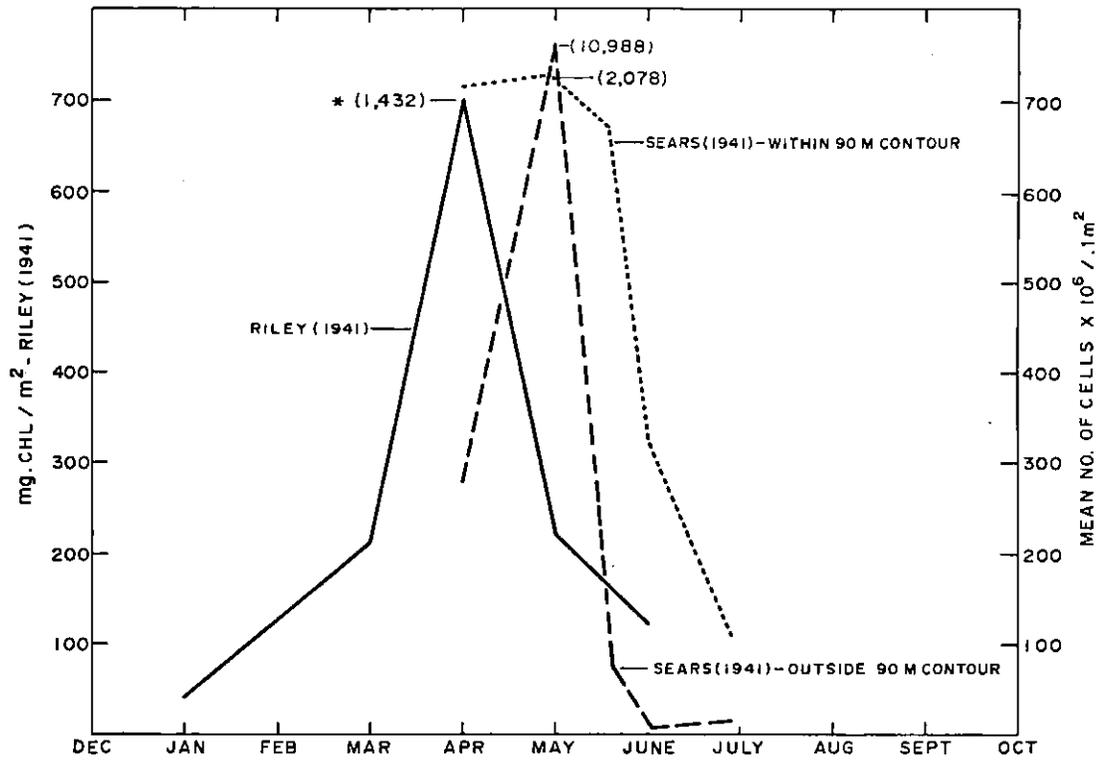


Fig. 9. Phytoplankton abundance on Georges Bank. (* = values exceed graph scale.)

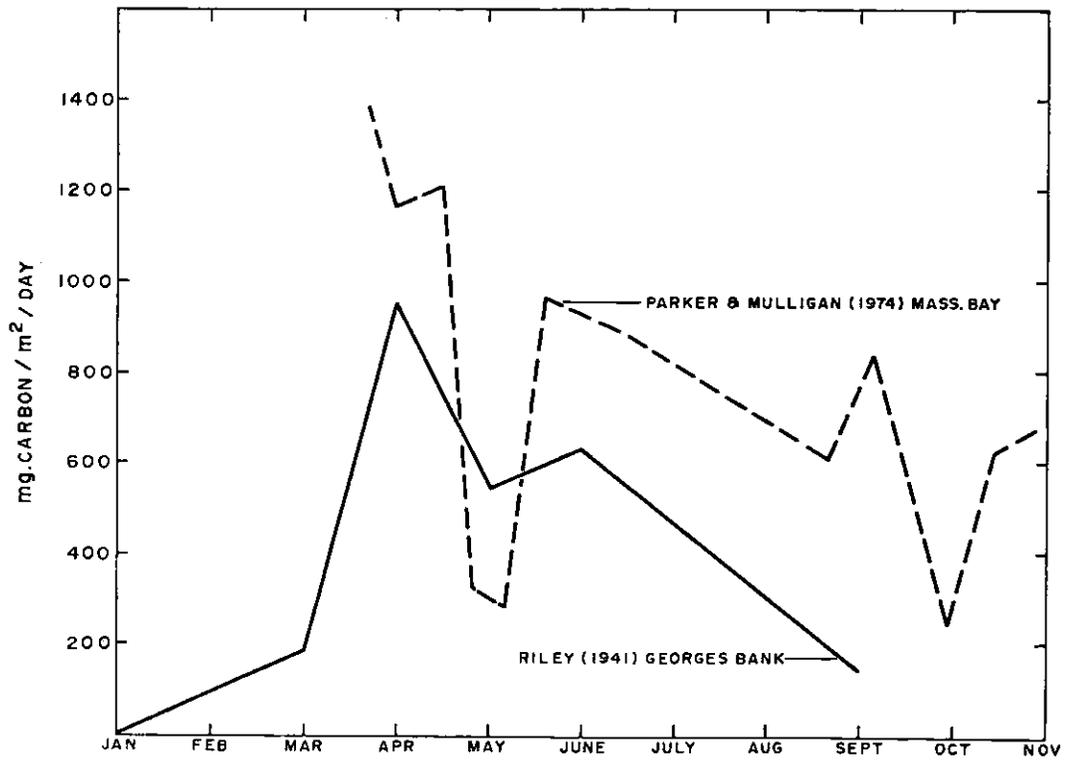


Fig. 10. Primary productivity in the Gulf of Maine.

During the winter the lowest values of biomass (2×10^6 cells/0.1 m², 40 mg Chl/m² and primary production (0 g C/m²/day) are observed, although the exact time may vary from year to year. Besides the yearly variations there are also differences from place to place within the Gulf of Maine (Bigelow *et al.*, 1940). The phytoplankton minimum occurs in December in the deep basin, western coastal region and on Georges Bank, while on the eastern side of the Gulf the phytoplankton minimum occurs in January (Bigelow *et al.*, 1940).

The spring bloom begins in late February to the middle of March in the coastal waters and on Georges Bank. At this time the biomass may be as high as $11,000 \times 10^6$ cells/0.1 m², and the primary production may reach values of 1.4 g C/m²/day. The bloom does not begin in the deep basin of the Gulf until April or even May (Bigelow *et al.*, 1940).

During the summer there is a decrease in the standing stock on Georges Bank (100 mg Chl/m² and 100×10^6 cells/0.1 m²) as well as for the Gulf of Maine as a whole (10×10^6 cells/0.1 m²). The data for Georges Bank (Fig. 9) do not cover the whole summer, but in the Gulf (Fig. 8) there is an increase in standing crop from June through September. Although the biomass on Georges Bank decreases drastically in the summer, the change in the primary production is less severe, decreasing to approximately 0.2 g C/m²/day in September. Riley (1941) did not continue his investigation past September. Parker and Mulligan's data (TRIGOM-PARC, 1974) from Massachusetts Bay indicated two moderate autumn blooms in 1973 (Fig. 10). Following the period of autumn activity, the standing stock and primary production reach their winter values.

Factors limiting primary productivity and biomass.

During the winter there is a plentiful supply of nutrients in the water (Bigelow *et al.*, 1940) but the depth of the mixed layer, due to wind and tidal mixing, greatly exceeds the critical depth (the critical depth is the depth at which the total community photosynthesis equals the total community respiration) (Sverdrup, 1953). On Georges Bank the mixed depth extends to the bottom but the critical depth lies above the bottom, due to the low level of solar insolation. As the season progresses the water column becomes more stable with increased solar radiation (and in coastal areas, increased runoff); at the same time the depth of the photic zone extends until the critical depth exceeds the depth of the mixed layer. Once this occurs the spring bloom will commence (Sverdrup, 1953). This does not happen until late February to mid-March in the coastal region and not until late April or even May in the deep basin of the Gulf (Bigelow *et al.*, 1940). The situation on Georges Bank is different. During the spring the water on Georges Bank is not stratified (Clarke *et al.*, 1943) but it is shallow enough for the mixed depth and critical depth to both be at the bottom; this usually takes place in late February to March.

During the summer, in the shallow areas and particularly on Georges Bank, the mixed layer extends to the bottom, insuring a steady supply of nutrients regenerated by bacterial action on the bottom. The existence of a pycnocline in the waters of the central basin, a condition necessary for the start of the bloom, restricts the flow of nutrients to the depleted surface waters from the nutrient rich waters at depth. Riley (1946), in his model of primary production for Georges Bank, used phosphate as the limiting nutrient, although phosphate is not usually considered as limiting phytoplankton growth in the marine environment (Roels *et al.*, 1971; Yentsch, 1975). Karaulovsky (1975) demonstrated that phosphate and nitrate were present in Georges Bank water during the summer. Bigelow *et al.*, (1940) postulated that nitrate was the limiting nutrient for the phytoplankton of the deep basin of the Gulf of Maine. However, Vaccaro (1963) has shown that in August, when nitrate concentration was lowest, ammonia was available in biologically significant quantities. There are probably additional sources of nitrogen that may also be important to phytoplankton in the Gulf of Maine. It has been demonstrated that urea (McCarthy, 1972; Carpenter *et al.*, 1972) and dissolved amino acids (Schell, 1974; Wheeler *et al.*, 1974) can be used by phytoplankton for growth. These sources of regenerated nitrogen (ammonium, urea and amino acids) are strong possibilities in the Gulf of Maine due to the large number of zooplankton grazing on the phytoplankton. Ketchum (1968) has observed that approximately half of the phosphorus requirements of the phytoplankton are met through the regeneration of nutrients. Nitrogen regeneration was not measured, but in other areas it was found to be significant (Jawed, 1973; LeBorgne and Binet, 1975). The large numbers of fish may also contribute regenerated nutrients (Whiteledge, 1975).

In view of the observations of Bigelow (1926) and Fish and Johnson (1937) on the enormous numbers of herbivorous zooplankton (in particular, *Calanus finmarchicus*), it is likely that zooplankton grazing limits the phytoplankton populations in the Gulf of Maine. Steele (1974) has postulated that herbivores limit phytoplankton growth in the marine environment. Cushing (1968) has shown this to be the case in a similar area where *Calanus finmarchicus* is the dominant zooplankton organism. The proposed mechanism for a grazing

limited bloom is as follows: in response to the spring phytoplankton bloom *Calanus finmarchicus* lays its eggs; after the eggs hatch the nauplii start to feed; and as the nauplii grow to adults they consume enough phytoplankton to decrease the standing stock. At present, there are not enough data to test this hypothesis for the central basin Gulf of Maine, i.e., if grazing is limiting the biomass of the phytoplankton, the primary production should remain fairly high. If, on the other hand, nutrients are limiting phytoplankton growth, both the biomass and the primary production should decrease.

From Fig. 10, it appears that grazing is limiting the magnitude of the bloom on Georges Bank. In Massachusetts Bay it appears that, after a brief bloom in April, nutrient limitation (nitrate concentration decreased to 0 mg-at/l, Frankel and Pearce, TRIGOM-PARC, 1974) causes a swift decline in primary production, followed by regeneration of nutrients, leading to another bloom in June which is limited by grazing. With the approach of autumn the stability of the water column decreases and mixing breaks down the pycnocline which results in an influx of nutrients into the surface waters. If several days of calm weather ensue, thus allowing the depth of the mixed layer to rise above the critical depth, a fall phytoplankton bloom is likely. The fall bloom will be smaller than the spring bloom (Riley, TRIGOM-PARC, 1946; 1974) and more variable as to the time of occurrence. After the autumn bloom, the depth of the mixed layer becomes greater than the critical depth and winter conditions prevail.

Average levels of primary production.

Based on Riley's (1941) paper, the yearly primary production of Georges Bank is approximately 120 g C/m²/year. His determinations were made using the oxygen production technique and are not as accurate as those obtained with the C¹⁴ technique (Steeman-Nielsen, (1963). Nevertheless this value of primary production is in reasonable agreement with observations made by Parker and Mulligan (TRIGOM-PARC, 1974) of about 200 g C/m²/year in Massachusetts Bay (another highly productive area in the Gulf of Maine). Values from similar coastal environments, by Steele (1974) working in the North Sea of 90 g C/m²/year and Ryther and Yentsch (Ryther, 1963) in the New York Bight area of 120 g C/m²/year at deep stations and 160 g C/m²/year in shoaler waters as well as the work of Emery and Uchupi (1972), suggest that the primary production in the Gulf of Maine is in the range of 100-200 g C/m²/year.

ZOOPLANKTON

Major surveys of the zooplankton of the Gulf of Maine have been carried out by Bigelow (1926) and Fish and Johnson (1937). Since then there have been numerous investigations, though usually on a smaller geographic scale, of the zooplankton in the Gulf (Clarke, 1933, 1934; Clarke and Zinn, 1937; Redfield, 1939, 1941; Redfield and Beale, 1940; Clarke *et al.*, 1943; Riley and Bumpus, 1946; Whitely, 1948; Colton *et al.*, 1962; Mullin, 1963; Pavshits, 1963; Pavshits and Gogoleva, 1964; Sherman, 1966a,b, 1968, 1970; Sherman and Perkins, 1971; Mauchline and Fisher, 1967; Grice and Hart, 1962). The following discussion of the zooplankton populations is an attempt to summarize, from the sources listed above and others, the annual zooplankton cycle in the Gulf of Maine.

Dominant species

The zooplankton of the deep basin of the Gulf of Maine has been characterized by Bigelow (1926) as a "Calanus community". This includes *Calanus finmarchicus*, *Pseudocalanus minutus*, *Metridia lucens*, *Sagitta elegans*, *Euthemisto*, *Thysoonoessa*, *Meganyctiphanes norvegica*, *Pleurobrachia pileus* and *Euchaeta norvegica*. The copepods, *Calanus finmarchicus*, *Pseudocalanus minutus*, *Oithona similis* and *Metridia lucens*, are the most abundant species in the Gulf of Maine (Fish and Johnson, 1937). *Calanus* may contribute up to 70% of the total zooplankton biomass (dry weight) and *Metridia* may be almost as important (Mullin, 1963). Other species that are numerically important members of the zooplankton during the year are *Centropages typicus*, *Anomalocera patersonii*, *Euthemisto compressa* and *Temora longicornis* (Fish and Johnson (1937). Bigelow (1926) and Fish and Johnson (1937) considered *Limacina retroversa* as an endemic species, but Redfield (1939) showed this to be an immigrant form that does not reproduce in the Gulf of Maine. The fauna on Georges Bank consists of a similar assemblage of species with the exception that *Calanus finmarchicus* does not occur and *Pseudocalanus* is the most abundant copepod. This is perhaps because of predation by the chaetognath, *Sagitta elegans*, that are present (Clarke *et al.*, 1943). *Sagitta elegans* is the only endemic chaetognath in the Gulf of Maine; *Eukrohnia lamata*, *Sagitta maxima* and *S. Lyra*, species that occur in abundance in the Gulf, are all carried in by deep currents and do not reproduce (Redfield and Beale, 1940). *Sagitta serratodentata* is an immigrant from the oceanic surface waters off the shelf (Redfield and Beale, 1940). The abundance of the deep-water chaetognaths is related

to their abundance offshore and to their longevity. *S. serratodentata* fluctuates in abundance in response to parcels of water entering the Gulf, probably in a manner similar to that observed for populations of *Limacina retroversa* (Redfield, 1939).

Reproduction cycles

Fish and Johnson (1937) found that reproduction of *Calanus finmarchicus*, *Pseudocalanus minutus*, *Thysanoessa* sp. and *Meganyctiphanes norvegica* starts in April in the western Gulf of Maine. For species such as *Calanus finmarchicus* (Fish, 1936a) and *Meganyctiphanes norvegica* (Fish and Johnson, 1937), the western coastal region is the principal source of the population. *Pseudocalanus minutus* and *Oithona similis* have their main area of reproduction in the outer Gulf and eastern basin (Fish, 1936b,c; Fish and Johnson, 1937). *Sagitta elegans* spawns on Georges Bank (Clarke *et al.*, 1940) and in the coastal waters of the western Gulf of Maine (Sherman and Schaner, 1968). *Sagitta* has an extended spawning period, spring through autumn, and produces one generation a year (Sherman and Schaner, 1968). Bigelow (1926) reports that the ctenophore, *Pleurobrachia pileus*, spawns in the shoal areas of the Gulf of Maine. This species is thought to spawn in late summer and autumn with the overwintering eggs that mature the following spring (TRIGOM-PARC, 1974). *Metridia lucens* does not appear to reproduce in the Gulf of Maine (Fish and Johnson, 1937). Bigelow (1926) proposed that *Metridia* was carried into the Gulf via Great South and Northeast Channels, and across Browns Bank. At various times of the year benthic larvae become important components of the zooplankton. For example, barnacle larvae (Fish and Johnson, 1937); Pavshtics and Gogoleva, 1964) *Mytilus* larvae (Fish and Johnson, 1937), and sea scallop larvae (Damkaer and Au, 1974) sometimes reach high localized densities.

Seasonal variations in species composition and biomass

Calanus is the first of the three most abundant species to reach its peak abundance (May), followed by *Pseudocalanus* (June) and then *Oithona* (August). During the summer, warm waters forms, such as salps, ctenophores and coelenterates, appear in the Gulf of Maine (Bigelow, 1926; Pavshtics, 1963). Pavshtics (1963) observed that with this change in the composition the quantity of food suitable for herring decreases. Bigelow (1926) noted that these organisms are predators on zooplankton, fish eggs and larvae. *Centropages typicus*, which in some years reaches great abundance in the fall, appears to be confined

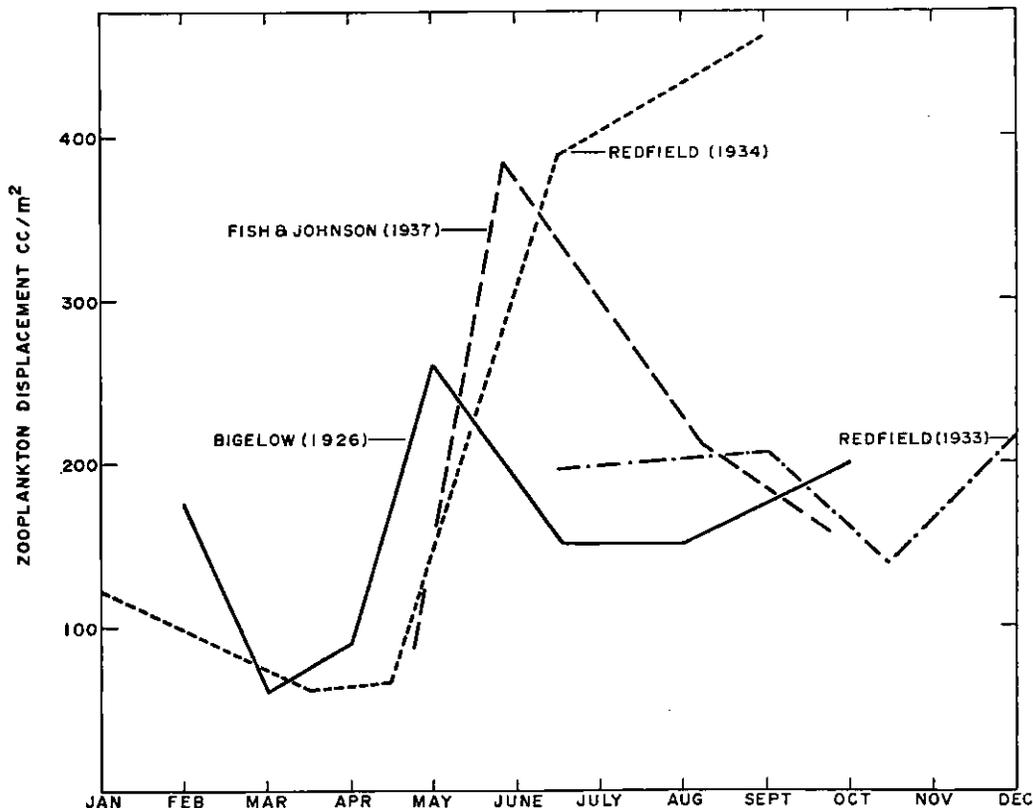


Fig. 11. Zooplankton displacement volumes in the Gulf of Maine.

to the inner Gulf, Bay of Fundy and Georges Bank. Fish and Johnson (1937) regard the Georges Bank population as separate from the population in the rest of the Gulf. The area of maximum zooplankton abundance shifts position with the season. From late summer to December zooplankton are most abundant in the northern portion of the Gulf, during the winter the center of abundance shifts to off the Massachusetts coast and in late spring and early summer it is found on the southern margin of the Gulf, Georges Bank and the western coastal region (Redfield, 1941).

The annual cycle of zooplankton biomass is represented in Fig. 11. Some of the variations observed between years is due in part to the sampling methods and gear used by the different investigators. The data should, however, present a gross picture of the seasonal cycle. Although all three investigators found an increase in zooplankton abundance in May, Bigelow (1926) and Fish and Johnson (1937) observed a decline during the rest of the summer. This pattern was also observed by Sherman (1970) for the coastal waters of the Gulf of Maine. This contrasts sharply with the picture presented by Redfield (1941) for the two years he sampled. He observed an increase during the course of the summer until September, although the levels reached in each year were markedly different. In order to get an idea of the probable cause of this increase, the circulation pattern in the Gulf of Maine and its effects on the zooplankton should be examined.

Zooplankton cycles in relation to circulation

Redfield (1941) has hypothesized that the surface waters flow in a great cyclonic eddy, augmented by inflow on the eastern side over the Scotian Shelf. Water is lost from the system to the southeast over Georges Bank. Colton and Temple (1961) found this loss of water over Georges Bank to be of such significance that they termed spawning and retention of larval fish on Georges Bank as an enigma. In the winter and early spring inflow replaces a considerable portion of the Gulf water with new water. Redfield (1941) feels that at least one-half of the zooplankton population of the Gulf of Maine is lost through this mechanism. Populations do not develop in this "new" water until spring, by which time this water extends over the northern half of the Gulf. The water in the southern region of the Gulf contains a rich flora from the previous summer, which has only been partially reduced during the winter. In spring and summer, inflow and outflow diminish and the water in the southern half of the Gulf is carried northeasterly. This results in the water starting its second trip around the Gulf carrying a rich fauna. This is an idealized picture, of course, and neglects lateral mixing, but the general pattern appears supported by Redfield (1939, 1941) and the physical oceanographic work of Bumpus and Lauzier (1965).

The volume of water entering and leaving the Gulf probably varies from year to year, due to changes in meteorological and oceanographic conditions. For example, Colton *et al.*, (1962), Pavshits and Gogoleva (1964) and Sherman (1966b), using oceanic copepods as indicators, reported on intrusions of slope water into the Gulf of Maine. It appears that most of the 'zooplankton poor water' enters the Gulf across the Scotian Shelf (Redfield, 1941). Redfield (1941) proposed that the population of the Gulf is impoverished in proportion to the amount of this water entering the area, since the inflow is proportional to the amount of zooplankton rich water leaving the Gulf of Maine. Sherman (1970) suggests that changes in the amount of water entering the Gulf from river discharge may be the cause of changes in the coastal zooplankton abundance from year to year. River discharge from the St. Lawrence may play a large role in the amount of water entering across the Scotian Shelf (Sutcliffe *et al.*, 1975). In years in which small amounts of low salinity water enters the Gulf, either across the Scotian Shelf or by direct river discharge, the surface salinity should be high, Redfield (1939) found that during the summer of 1934 the surface salinity in the Gulf of Maine was exceptionally high and so was the zooplankton biomass as compared with 1933 (Fig. 11).

The circulation of water is not only an important factor in the deep basin of the Gulf of Maine but on Georges Bank as well. Clarke *et al.*, (1943) observed that the distribution of *Sagitta elegans* on Georges Bank was restricted to the "mixed area". The "mixed area" was an area where "turbulence produced by tidal currents and by the wind in the relatively shallow water...causes a vertical mixing of the water which results in a nearly uniform distribution of temperatures and salinity from top to bottom... particularly in the central portion of the Bank" (Clarke *et al.*, 1943). *Sagitta serratodentata* and *S. enflata* were abundant outside this zone but never within it. A similar distribution was observed for *Calanus* and *Pseudocalanus*, the latter occurring within the "mixed area" but the former only in the stratified waters surrounding the "mixed area" (Clarke *et al.*, 1943)

Sherman (personal communication) has proposed that the seasonal changes in zooplankton abundance are the result of local fluctuations in water temperature and stability rather than large scale circulation. Lasker (In press) has shown that the stability of the water column plays an important role in the survival of anchovy larvae. He found that the first feeding larvae are dependent on chlorophyll maximum layers, which are only present when the water column is stable. Not only must there be a dense enough aggregation of phytoplankton in the chlorophyll maximum but the size and species composition are also critical. For example, if the organisms present were too small (optimum food size is approximately 50μ) or of a species such as *Chaetoceros* (with numerous spines), the larvae did not feed.

A similar mechanism with respect to zooplankton may exist in the Gulf of Maine. Copepod fauna in the Gulf of Maine is characterized by swarms of nauplii and copepodites after the spring phytoplankton bloom (Bigelow, 1926; Sherman, 1970). If the stability of the water column is destroyed and the dense patches of phytoplankton bloom are dispersed (e.g. by a series of storms), the young copepods may not be able to obtain enough food to survive.

FUTURE RESEARCH

There is a need for further quantitative studies of primary and secondary productivity to provide a better basis for relating these phases of organic production to potential fish production.

From the standpoint of gaining insight into the factors controlling the survival of larval fish, a better understanding of zooplankton dynamics, especially predator-prey interactions between larval fish and zooplankton, must be achieved. Pavshatics (1963) has reported that, when the species composition of the zooplankton changed from copepods to salps and ctenophores, this food was less suitable to herring. Several investigators have shown that copepods are the predominant food organism of young herring (Sherman and Honey, 1971; Sherman and Perkins, 1971; Damkaer and Au, 1974), young cod, haddock, coalfish (Marak, 1960) and young redbait (Marak, 1974). An area that may be of great importance to larval fish survival is the predation on them by zooplankton (Lillelund and Lasker, 1971; Theilacker and Lasker, 1974), especially by *Sagitta*, ctenophores and coelenterates (Bigelow, 1926). *Sagitta* and ctenophores, such as *Pleurobrachia pileus*, may be of special importance to larval herring, since they are both abundant in the Gulf of Maine at the time herring spawning occurs.

A useful first step in the investigation of zooplankton populations in relation to the growth and survival of herring larvae would be to fully sort and analyze the invertebrate components of the larval herring survey samples, in conjunction with an examination of the herring gut contents. This analysis should include a look at the abundance of smaller zooplankton, as well as nauplii and copepodites of larger forms, collected with the fine mesh nets. This will provide an estimate of the abundance of potential predators on the larvae as well as quantifying the abundance of food organisms for the larvae. In addition, comparing the gut contents with the abundance of food types available will yield insight into possible selectivity of preferred prey. The area of larval fish mortality studies, including recommendations for future research, has recently been discussed in a colloquium on Larval Fish Mortality and Fishery Research, held in January 1975 at LaJolla, California.

In order to understand the role that the zooplankton play in the transfer of energy to higher trophic levels, an investigation of the effects of zooplankton on the phytoplankton community (including regeneration of nutrients and grazing) is needed. The effect that various physical factors (such as the loss of water from the Gulf of Maine gyre over Georges Bank) and biological factors (such as the timing and species composition of the phytoplankton blooms) have on the abundance and life cycles of the zooplankton need to be delineated.

Although zooplankton dynamics is the more immediate and difficult area of concern, better information on the primary productivity of the Gulf of Maine, including the effects of biotic and abiotic factors on primary production is needed. Primary production studies in various parts of the Gulf, such as Georges Bank, the coastal region and the deep basin, are necessary to refine the range $100-200\text{ g C/m}^2/\text{year}$, so that estimates of the production at higher trophic levels (similar to those of Steels, 1974) can be refined. For example, if the average value of $150\text{ g C/m}^2/\text{year}$ is used for primary production on Georges Bank, and a conversion efficiency of 15% is used between trophic levels, then $0.51\text{ g C/m}^2/\text{year}$ will be the production at the fourth trophic level (fish). This is well above the minimum finfish production of $0.19\text{ g C/m}^2/\text{year}$ based on fish catch (Clark and Brown, 1975) for

Georges Bank. This calculation represents only a rough estimate for several reasons: (1) a straight food chain has been assumed rather than a food web which would reduce the yield to a given trophic level (Steele, 1974); (2) the food chain consists of only phytoplankton → zooplankton → carnivores → fish, but, if the nanoplankton play an important role in the primary production of the Gulf, an additional level of microzooplankton is necessary (Parsons and Lebrasseur, 1970); (3) a conversion efficiency of 15% has been assumed and this might not be the actual value.

In order to gain a better understanding of the fish production that can be supported by a given amount of primary production the structure of the food web must be elucidated, and improved knowledge on the contributions of bacteria, dissolved organic carbon and particulate organic material (detritus) is needed.

It is possible to use knowledge about the productivity of the lower trophic levels to estimate fish production (for a comprehensive discussion of the need and problems involved in obtaining estimates of this type, see Dickie, 1971). Au (1973) has attempted to estimate the maximum finfish yield from ICNAF Subarea 5 and 6, using primary productivity data. An increased knowledge of the energy pathways at the lower trophic levels of the food web will lead to a theoretical basis for deriving a limit of fish catch, such as that used in the second-tier TAC.

The areas of investigation outlined in this section are not meant to be a definitive list of the biological oceanographic studies needed in the Gulf of Maine. They should be viewed only as a place to start in obtaining information on the plankton communities that will be useful in fisheries management.

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Catch and Effort Relationships of the Groundfish Resource in ICNAF Subareas 2 and 3¹

by

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ABSTRACT

Analysis of catch and effort data from the groundfish fishery in ICNAF Subarea 2 and Division 3K and in Divisions 3LNOP during 1959-73 revealed that catches peaked in the northern area in 1968 and in the southern area in 1967 and have declined since then. Cod was the most important species in both areas although more so in the northern area.

Fishing effort generally doubled over this period and catch per unit effort declined by about one-half. Effort remained high after the period of peak catches although catches declined to earlier levels. General production models for both areas indicated that fishing effort generally has been beyond the MSY (maximum sustainable yield) level in the northern area since about 1967 and has been close to or beyond the MSY level in the southern area. When increases in efficiency were incorporated into the models, the resultant fishing effort estimates were almost all above the MSY level after 1966.

INTRODUCTION

In view of the discussion at present taking place in ICNAF on a proposal to reduce fishing effort on groundfish in Subareas 2 to 4, the present paper provides background data on the catch, effort and catch per unit effort for the groundfish resources in Subareas 2 and 3.

MATERIALS AND METHODS

Since almost all of the groundfish catch in Subarea 2 and Div. 3K is composed of cod whereas a broader spectrum of species appear in the groundfish catch in Div. 3L, 3N, 3O and 3P, the catch and effort data were analyzed for the two regions separately (Fig. 1).

The basic data for catch and effort analyses were taken from the tables of basic effort statistics in the ICNAF *Statistical Bulletin* for the years 1959 to 1973, with data for 1955-58 being used in certain cases. The general approach was to combine the catch and effort data of the various countries for each vessel tonnage category, where there had been continuing and significant fisheries in the areas, in order to provide standardized catch per unit effort values for the various vessel tonnage classes. These standardized values formed the basic data for general production model studies.

General production curves were constructed using a range of running averages of fishing effort to account for the time lag in response of the resource to changes in fishing effort. The averaging period producing the highest correlation coefficient (r) for a given area for all standards was chosen as best describing the data. This was a period of 7 years for Subarea 2 and Div. 3K data and 6 years for Div. 3LNOP data.

¹ Submitted to 1975 Annual Meeting as Res.Doc. 75/55.

The production curves did not take into consideration the increases in efficiency which must have occurred in the 1955-56 to 1973 period due to increases in size and power of vessels within tonnage categories, gear and navigational and acoustic equipment improvements, and improvements in vessel design. To allow for these changes, a steady rate of increase in efficiency was introduced into the model. Running averages of effort were varied commencing at 1 year and increases in efficiency commencing at 0% until the combination of running average and increase in efficiency which produced the highest correlation coefficient was obtained for each effort standard (Table 5, Fig. 11 and 12).

RESULTS

Subarea 2 and Division 3K

The total groundfish catches by country for this area are given in Table 1 and the catches of the major groundfish species are given in Table 2. These data are illustrated graphically in Fig. 1 and 2.

Fig. 3 shows catch rates of the country-tonnage categories used as standards. Although catch rates between countries are considerably different in some of the earlier years, and, although trends in catch rates are different for different countries over the period 1959-73, ranging all the way from an almost continuous decline in catch per day fished from 1962-73 for France (900-1800 GRT¹) to no real trend for Poland, one feature common to almost all countries is the decline in the catch per day fished since the late 1960's. Some of this may have been caused by severe ice conditions in recent years, but some of it must have been because of the high catches in the 1968-69 period which reduced stock size.

Fig. 4 shows the catch, standard effort and catch per standard effort for two tonnage classes (901-1800 and >1800 GRT). The decline in catch per effort since 1962-63, and especially since 1968-69, is evident, as is the approximate doubling of the fishing effort between the early 1960's and the late 1960's and early 1970's. It is also obvious that the fishing effort for some categories has been maintained in the period after 1968 even though the catch has declined.

Since one of the complicating factors in this northern area is the change in seasonal pattern of fishing over the 1959-73 period from a summer-autumn fishery in the early years to a more productive winter-spring fishery in the later years, a seasonally adjusted index of abundance was also used. The index used was derived by J.G. Pope (personal communication) and is based on the catch per unit effort for cod in the Spanish otter trawl fishery. This cod catch per hour, expressed in terms of the catch per hour in March, was divided into the total groundfish catch to provide seasonally adjusted standard effort figures for 1959-73. It was felt that, since the cod catch represents such a large part of the groundfish (Fig. 4), this was a valid standard unit of effort. The increasing effort trend and decreasing catch per unit effort trend is also obvious with this standard effort unit.

Two of the units of effort described above were used to construct general production curves as is shown in Fig. 5 and 6. The correlation between catch per unit effort and effort for the >1800 GRT category was not significant and therefore the production curve was not constructed. A seven-year averaging period was used and correlations of catch per effort versus average effort were significant. These yield curves generally show that the catch and effort fluctuated around the MSY level during 1959-73. The general conclusion is that there was more than enough effort to take the MSY catch during the 1970's. The MSY for the groundfish resource as a whole is estimated at about 400,000 tons.

When best estimates of steady increases in efficiency of the fleets were incorporated into the model (Table 5), the general result was a shift in the effective fishing effort in each case further beyond the MSY level and to improve the correlation coefficient. MSY estimates remained the same as before (275,000 to 400,000 tons), but the results now indicated that fishing effort has been beyond the MSY level since 1967-68.

Divisions 3L, 3N, 3O and 3P

The total groundfish catches by country for this area are given in Table 3 and the catches of the major groundfish species are given in Table 4 (see also Fig. 1 and 2).

Fig. 7 shows the catch rates of the country-tonnage categories used as standards. Again, catch rates between countries are different in certain years for the same category,

¹ GRT = gross registered tonnage

Table 1. Total nominal catches of groundfish by country for Subarea 2 and Div. 3K, 1959-73¹.

Year	CAN(M)	CAN(N)		FRA(M)	FRG	Non-mem	ICE	NOR	POL
		(Inshore)	(Offshore)						
1959	-	75,700	-	45,265	38,187	7,834	66,573	50	232
1960	53	64,400	3	60,607	42,777	5,811	5,077	45	-
1961	3	50,500	1	54,572	28,413	-	4,692	217	582
1962	-	68,000	-	54,686	4,835	7	2,297	-	3,263
1963	-	73,000	2	52,700	3,259	5	5,199	-	17,450
1964	-	57,400	19	57,166	13,871	19,585	2,762	-	34,493
1965	297	55,200	29	39,646	44,816	54,937	2,738	827	41,034
1966	-	60,100	57	48,867	70,474	73,191	2,936	863	49,359
1967	219	55,900	241	52,744	33,938	72,837	2,201	2,022	54,564
1968	365	65,500	7,287	64,873	55,160	-	397	8,157	102,880
1969	-	38,500	365	39,824	72,612	3,317	359	7,036	88,466
1970	-	35,100	1,070	17,743	62,415	-	-	4,145	66,506
1971	-	33,900	589	6,416	30,452	19,067	283	7,743	44,999
1972	-	24,000	371	8,838	30,292	30,699GDR	306	9,034	54,815
1973	-	24,600	739	4,153	42,115	29,987GDR	-	7,749	47,139

Year	POR	SPA	USSR	UK	Others	Total		Total catch
						offshore catch	inshore catch	
1959	34,714	30,198	91,959	2,525	6	317,543	75,700	393,243
1960	59,806	42,123	149,519	1,144	810	367,775	64,400	432,175
1961	65,089	53,345	160,671	1,652	-	369,237	50,500	419,737
1962	75,872	67,027	87,033	4,271	-	299,291	68,000	367,291
1963	103,439	65,666	45,201	706	-	293,627	73,000	366,627
1964	79,297	72,934	85,040	1,934	-	367,101	57,400	424,501
1965	85,946	69,432	72,008	14,736	-	426,446	55,200	481,646
1966	58,773	57,932	45,884	16,507	-	424,843	60,100	484,943
1967	65,737	46,541	61,494	18,307	-	410,845	55,900	466,745
1968	72,848	46,672	195,183	23,690	-	577,512	65,500	643,012
1969	79,512	45,123	204,741	3,729	2,300	547,384	38,500	585,884
1970	49,828	16,089	137,635	2,832	6,106	364,369	35,100	399,469
1971	39,786	10,503	177,776	397	2,976	340,987	33,900	374,887
1972	27,386	5,052	211,860	5,155	3,129	386,937	24,000	410,937
1973	42,249	4,188	129,180	4,683	4,819	317,001	24,600	341,601

¹ Some catches by countries which reported no fishing effort in ICNAF *Statistical Bulletin* are not included in the total groundfish catch. Abbreviations for countries are the same as used in *Statistical Bulletin*.

Table 2. Nominal catches of major groundfish species for Subarea 2 and Div. 3K.

Year	Cod	Haddock	Redfish	Plaice	Witch flounder	Yellowtail flounder	Greenland halibut	Roundnose grenadier	Total
1959	199,261	109	186,837	-	-	-	-	-	386,207
1960	306,327	28	129,773	16	158	-	-	-	436,302
1961	356,718	135	55,455	67	87	-	613	-	413,075
1962	343,573	163	19,657	61	38	-	481	-	363,973
1963	338,539	172	23,644	119	5	-	602	-	363,081
1964	364,385	30	50,154	122	2	-	2,807	-	417,500
1965	405,409	60	40,245	230	34	-	2,653	-	448,631
1966	427,641	48	32,730	238	1,092	-	5,139	-	466,888
1967	399,728	190	26,162	407	365	-	6,085	17,094	450,031
1968	607,225	9	18,881	1,023	282	-	9,447	30,657	667,524
1969	556,396	39	24,606	1,906	865	-	31,917	12,779	628,508
1970	315,999	48	21,797	12,686	15,712	1	30,788	24,299	421,330
1971	242,767	143	19,306	5,348	10,448	5	19,027	75,390	372,434
1972	309,636	32	20,033	9,121	13,258	10	25,208	24,231	401,529
1973	230,975	455	38,965	5,140	18,698	549	25,381	17,399	337,562

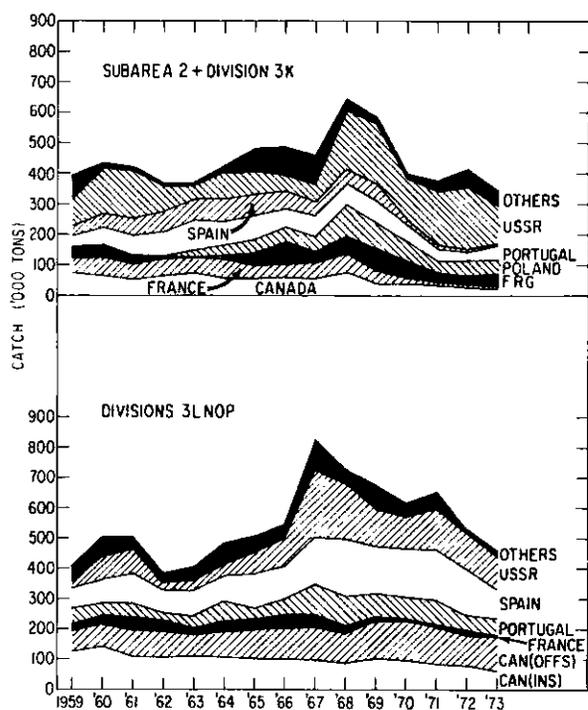


Fig. 1. Nominal catches of groundfish by country for two major regions in Subareas 2 and 3, 1959-73. (OFFS = offshore; INS = inshore.)

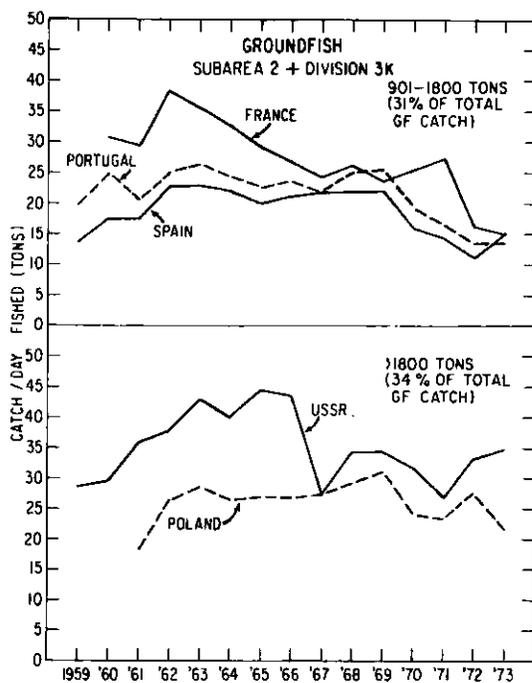


Fig. 3. Catch rates of country-vessel tonnage classes used as standards for Subarea 2 + Div. 3K, 1959-73.

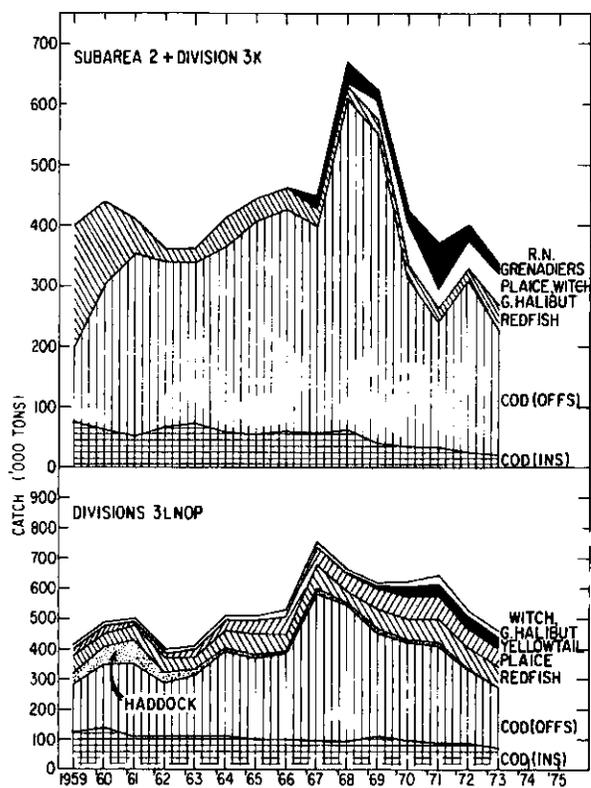


Fig. 2. Nominal catches of major groundfish species for the two regions of Subareas 2 and 3, 1959-73. (OFFS = offshore; INS = inshore.)

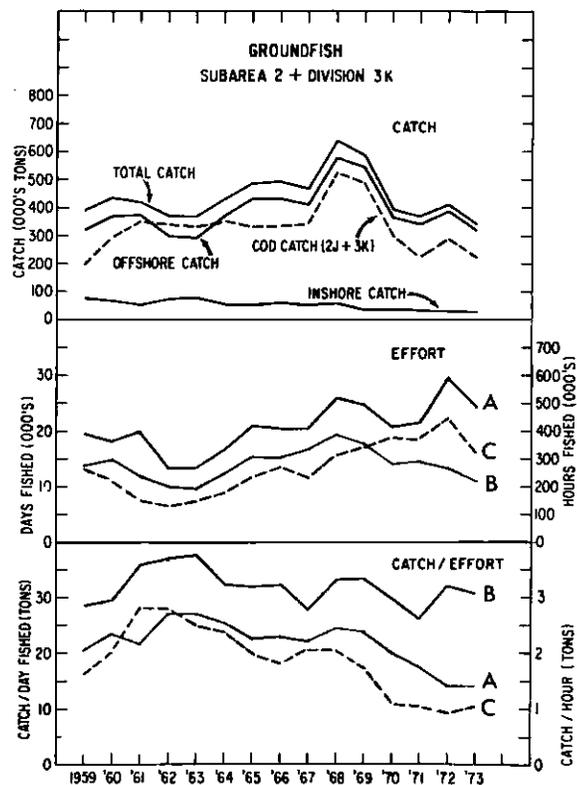


Fig. 4. Catch, effort and catch per unit effort for groundfish in Subarea 2 + Div. 3K, 1959-73. (A = groundfish catch per day for 901-1800 GRT; B = groundfish catch per day for >1800 GRT; C = adjusted cod catch per hour for Spanish OT.)

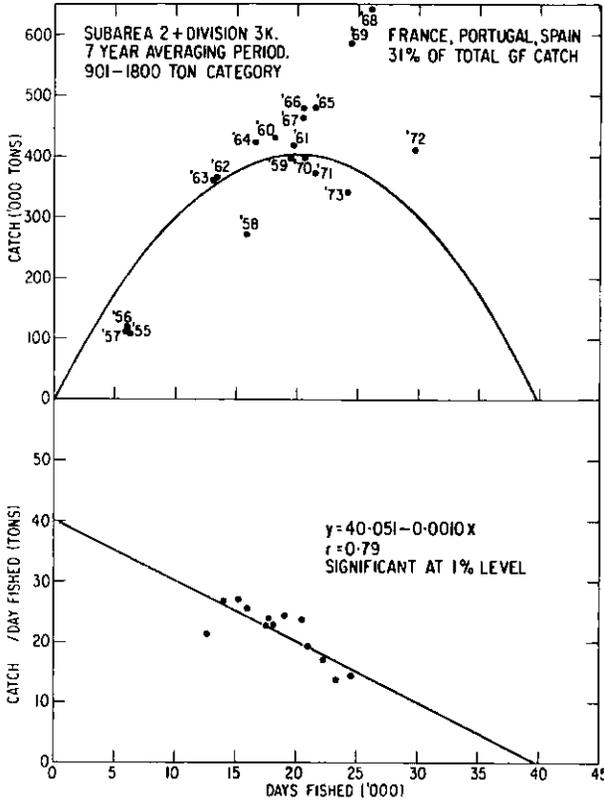


Fig. 5. Yield curves for total groundfish resource in Subarea 2 + Div. 3K, based on catch per unit effort of 901-1800 GRT as standard.

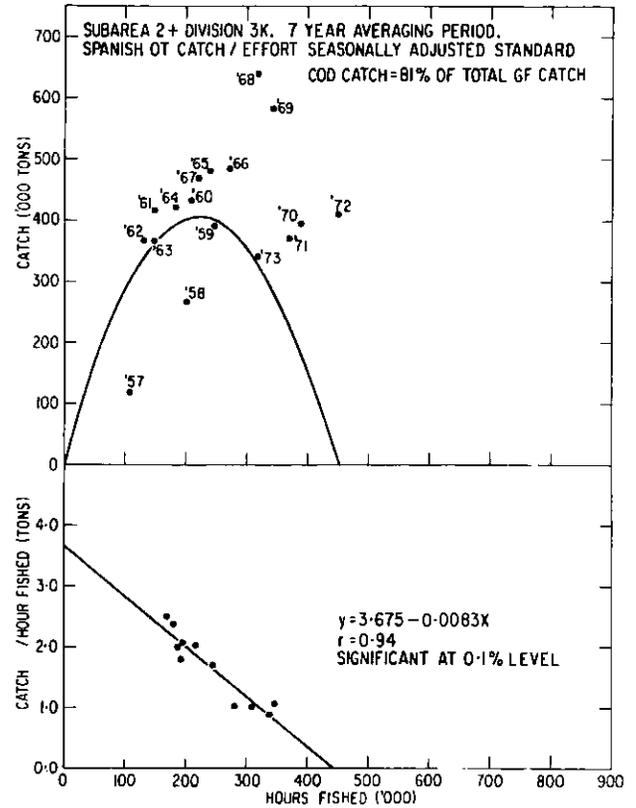


Fig. 6. Yield curves for total groundfish resource in Subarea 2 + Div. 3K, based on catch per unit effort of Spanish OT as standard.

and trends in catch rates over the period are different for different countries, ranging all the way from an almost continuous decline for France (901-1800 GRT) to very little trend at all for Poland (>1800 GRT). However, almost all country-tonnage categories exhibited a decline in catch per effort from about 1967-68 to 1973, after the period of high catches in 1967-68. This is also obvious in Fig. 8, as is the fact that fishing effort increased between 1959-66 and 1967-72 and was maintained at this level even though catches declined. There is an indication of some decline in 1972-73 for the 151-500 and >1800 GRT categories and in 1973 for the 901-1800 GRT category.

The effort standards for the 151-500 and 901-1800 GRT categories were used to construct the general production curves of Fig. 9 and 10. A six-year averaging period for effort produced significant correlations of catch per day fished versus average of days fished. Both curves indicate that fishing effort was somewhat below that necessary to take the MSY during 1959-66 but was at least equal to that necessary to take the MSY during 1967-72 (151-500 GRT category) and may have exceeded it (901-1800 GRT category). Using the effort standards for the 151-500 GRT vessel category indicates that effort in 1972-73 was less than that necessary to take the MSY, whereas the data for the 901-1800 GRT category indicate that the effort was at least equal to that necessary to take the MSY in 1973 and beyond that level in 1972. The MSY for this southern region is estimated to be about 600,000 tons.

When best estimates of increases in efficiency are incorporated into the model (Table 5), the MSY estimates ranged from 525,000 to 590,000 tons and fishing effort was beyond that necessary to take the MSY in each year since 1966. In each case the correlation coefficient was higher than that obtained without consideration of efficiency factors.

Table 3. Total nominal catches of groundfish by country for Div. 3LNOP, 1959-73¹.

Year	CAN(M)	CAN(N)		DEN(F)	FRA(M)	FRA(STP)	FRG	Non-mem	NOR	POL
		(Inshore)	(Offshore)							
1959	26,767	124,000	42,006	7,618	17,105	7,746	9,929	2,600	4,470	-
1960	30,069	140,200	46,489	9,678	22,702	6,783	6,913	5,591	5,258	400
1961	27,410	108,600	56,624	5,526	34,226	9,700	4,617	-	3,081	2,817
1962	21,231	109,700	60,065	4,592	34,743	5,788	274	339	1,897	3,106
1963	12,325	111,500	55,916	14,003	14,600	6,877	1,593	1,299	1,831	2,908
1964	18,441	108,800	58,809	-	36,583	5,631	537	42,785	6,249	1,675
1965	15,802	100,800	76,564	9,717	35,155	6,122	9,429	16,679	29	3,596
1966	22,022	100,900	84,033	14,908	31,288	8,171	6,616	7,935	211	5,313
1967	17,516	97,900	87,763	15,539	34,982	7,750	1,005	32,200	4,037	18,037
1968	12,526	90,500	84,590	17,123	21,658	3,627	-	880	11,913	1,687
1969	15,908	104,500	102,650	18,856	11,649	3,225	-	74	53,878	1,725
1970	20,996	95,000	108,526	9,562	3,834	4,495	-	-	35,534	587
1971	17,857	87,500	97,929	14,227	5,782	3,570	189	7,843	18,941	3,369
1972	15,273	82,400	85,394	-	8,530	3,655	69	584GDR	6,280	3,903
1973	11,313	62,800	99,520	1,802	2,598	2,810	2,294	1,720GDR	1,542	8,480

Year	POR	SPA	USSR	UK	USA	Others	Total		Total catch
							offshore catch	inshore catch	
1959	45,534	68,968	25,574	2,634	16,570	3,890	281,411	124,000	405,411
1960	40,151	78,198	74,620	10,539	15,245	8,357	360,993	140,200	501,193
1961	49,525	96,607	81,380	8-231	16,722	134	396,599	108,600	505,199
1962	22,628	73,637	24,191	5,945	14,264	339	273,039	109,700	382,739
1963	43,502	84,695	29,923	10,789	10,470	-	290,731	111,500	402,231
1964	60,740	89,529	33,521	16,716	4,202	594	376,012	108,800	484,812
1965	34,383	114,540	65,330	19,840	772	609	408,567	100,800	509,367
1966	49,934	113,153	89,151	13,885	347	885	447,852	100,900	548,752
1967	96,506	159,172	221,888	30,056	149	-	726,600	97,900	824,500
1968	95,943	187,693	186,199	11,650	199	-	635,688	90,500	726,188
1969	78,126	158,758	122,849	1,295	76	-	569,069	104,500	673,569
1970	73,212	161,803	102,724	314	55	3,343	524,985	95,000	619,985
1971	81,311	168,590	134,253	4,524	-	6,441	564,826	87,500	652,326
1972	53,229	152,168	113,615	3,693	-	2,124	448,517	82,400	530,917
1973	54,753	103,198	101,105	1,329	-	3,335	395,799	62,800	458,599

¹ Some catches by countries which reported no fishing effort in ICNAF *Statistical Bulletin* are not included in the total groundfish catch.

Table 4. Nominal catches of major groundfish species for Div. 3LNOP, 1959-73¹.

Year	Cod	Haddock	Redfish	Plaice	Witch flounder	Yellowtail flounder	Greenland halibut	Total
1959	279,045	34,967	59,835	(19,919) ¹	(2,827) ¹	(45) ¹	(772) ¹	397,410
1960	346,383	60,585	44,009	22,217	7,272	8	-	480,474
1961	348,572	79,386	44,345	17,874	5,823	151	143	496,294
1962	284,754	35,077	42,440	17,264	5,831	90	116	385,572
1963	310,179	14,344	44,129	25,610	3,259	143	195	397,859
1964	390,932	11,207	57,561	38,995	2,252	226	908	502,081
1965	369,578	7,983	65,926	49,492	2,087	3,129	6,055	504,250
1966	379,945	9,771	53,147	55,699	5,365	4,317	12,589	520,833
1967	581,616	11,373	79,216	59,268	8,147	2,183	13,915	755,718
1968	541,003	6,540	37,951	55,185	5,161	5,001	9,779	660,620
1969	447,981	5,321	73,288	69,276	4,406	10,564	5,660	616,496
1970	419,462	7,115	65,023	78,980	12,057	26,898	6,146	615,681
1971	409,622	5,034	81,695	75,141	22,844	37,681	5,583	637,600
1972	321,157	3,575	71,087	66,301	15,932	39,671	4,894	522,617
1973	268,201	1,874	60,462	67,792	15,412	33,749	3,781	451,271

¹ Estimated from Subarea 3 totals.

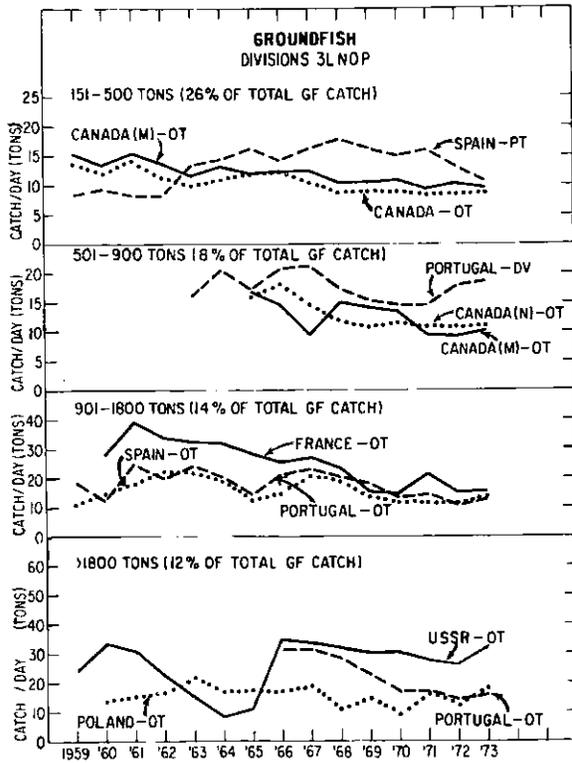


Fig. 7. Catch rates of country-vessel tonnage classes used as standards for Div. 3LNOP, 1959-73.

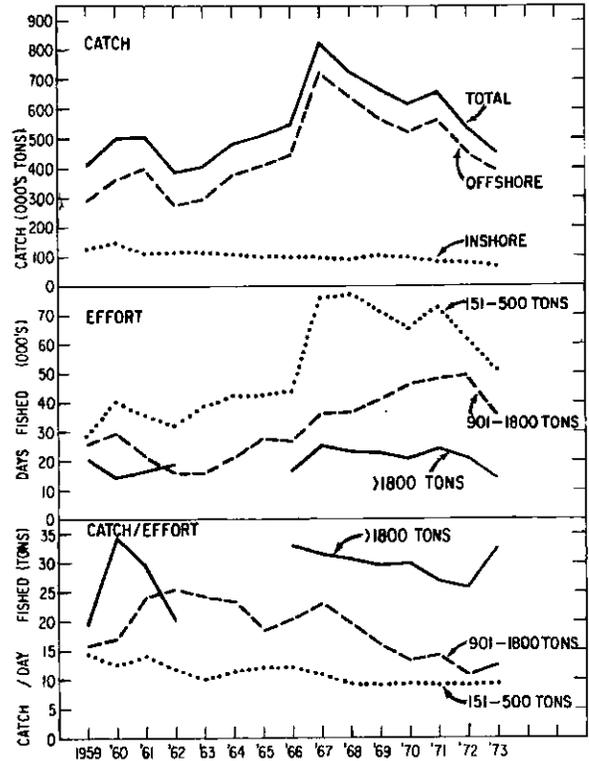


Fig. 8. Catch, effort and catch per unit effort for groundfish in Div. 3LNOP, 1959-73.

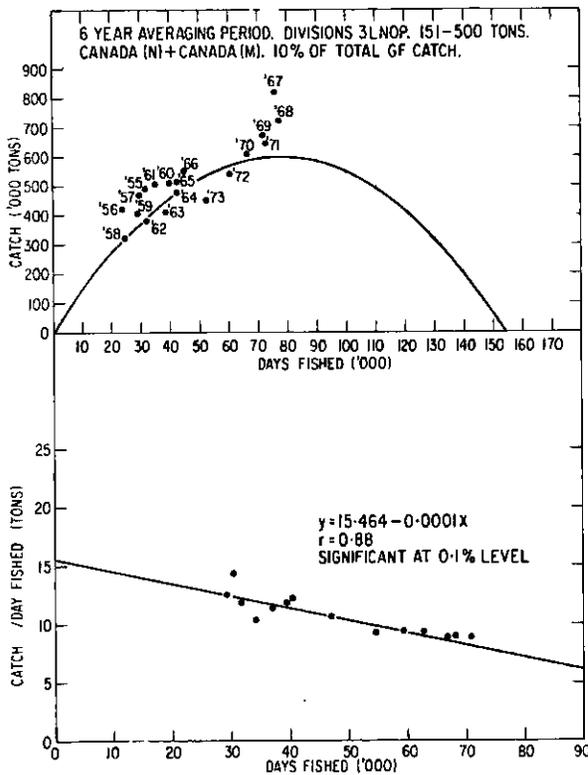


Fig. 9. Yield curves for total groundfish resource in Div. 3LNOP based on catch per unit effort of 151-500 GRT OT as standard.

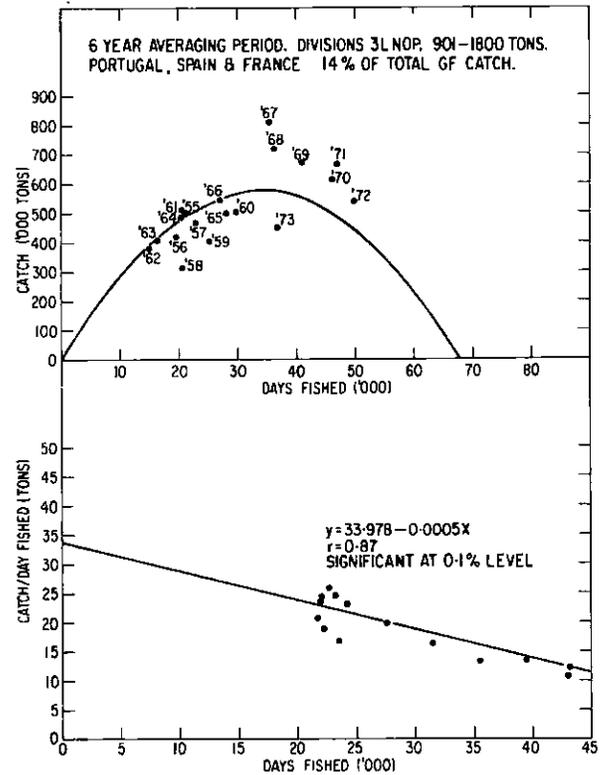


Fig. 10. Yield curves for total groundfish resource in Div. 3LNOP based on catch per unit effort of 901-1800 GRT OT as standard.

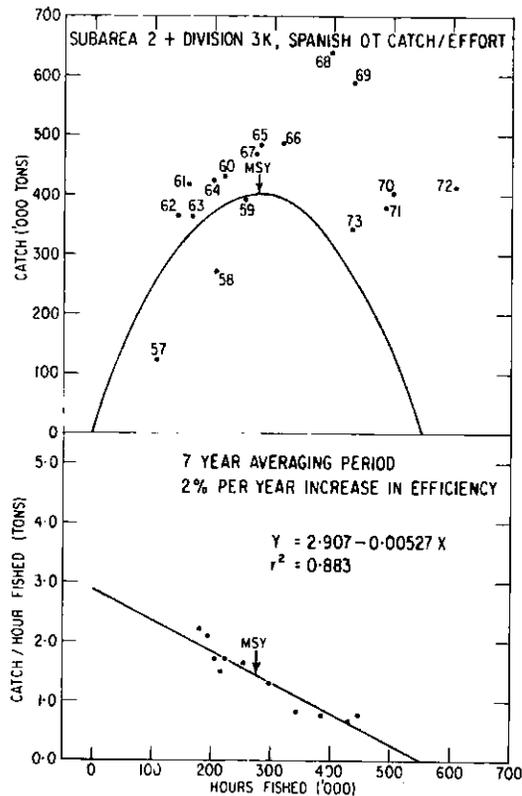


Fig. 11. Yield curves for total groundfish resource in Subarea 2 + Div. 3K, using 7 years for effort and a constant increase in efficiency of 2% per year (giving highest r^2).

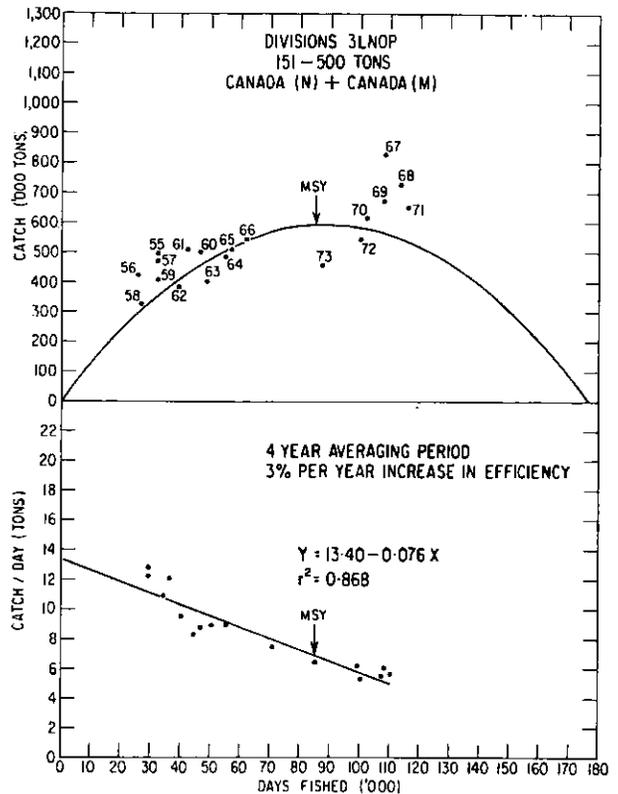


Fig. 12. Yield curves for total groundfish resource in Div. 3LNOP using 4 years for effort and a constant increase in efficiency of 3% per year (giving highest r^2).

CONCLUSIONS

The Schaefer production model indicated that the MSY in Subarea 2 and Div. 3K is unlikely to be greater than 400,000 tons and is probably less than this. The lowest estimate of MSY with increases in efficiency incorporated was 375,000 tons. The estimated MSY for Div. 3LNOP is unlikely to be greater than 600,000 tons and could be as low as 525,000 tons. Table 5 indicates that, for all of the fishing effort standards used, the fishing effort adjusted for increases in efficiency has been beyond that necessary to generate the MSY catch in every year in the 1967-73 period, except in the case of the effort standard for Spanish otter trawlers in Subarea 2 and Div. 3K in 1967 and for the 151-500 GRT category in Div. 3LNOP in 1973. In Subarea 2 and Div. 3K, fishing effort in 1973 could have been 30-60% above the level necessary to attain the MSY catch, whereas in Div. 3LNOP the effort in 1973 was at least high enough to attain the MSY level of catch and could have been 25% above it. Some of the apparent reduction in groundfish effort in 1973 for both areas probably resulted from a diversion of groundfish effort to fishing for capelin in that year.

Total allowable catches (TACs) for groundfish species in Subareas 2 and 3, set for 1975, sum to 1,089,000 tons. In addition, some 30,000 tons of unregulated groundfish can be expected to be caught in 1975, indicating a total catch of 1,119,000 tons if all TACs are caught. Bearing in mind that some increase in efficiency has certainly occurred, the groundfish MSY for Subareas 2 and 3 is unlikely to be greater than 1,000,000 tons and is probably less than this; the lowest estimate from the Schaefer model is 900,000 tons.

Data on 1974 catch rates of Newfoundland-based bottom otter trawlers indicate a decline in catch rate of 14% between 1969 and 1973 and a decline of 19% between 1973 and 1974, for a total decline of 30% between 1969 and 1974. This indicates a continuing decline in population abundance.

Table 5. Groundfish MSY catch and effort from combinations of averaging periods and increases in efficiency producing best correlations of CPUE versus effort. Adjusted effort for each of the years 1967-73 is given together with the averaging periods and % efficiency increases giving best correlations (r^2). (DF = days fished; HF = hours fished.)

Area	Vessel category used as standard	Effort units used	MSY		Adjusted effort in each year							Averaging period (1) and % increase in efficiency (2) for best r^2		r^2	% effort reduction from 1973 level to MSY level
			Catch	Effort	1967	1968	1969	1970	1971	1972	1973	(1)	(2)		
2+3K	Spain-OT ¹	HF	398	275	271.1	394.1	434.9	494.3	487.0	604.2	431.4	7	2	0.8826	30
	901-1800	DF	378	25	32.9	43.5	42.5	37.0	40.3	58.0	48.9	8	4	0.9704	59
	>1800	DF	375	37	42.9	55.8	54.9	48.1	56.4	55.3	52.5	7	11	0.9161	30
3LNOP	151-500	OF	590	85	107.8	112.9	107.5	101.6	115.8	100.0	86.6	4	3	0.8678	2
	901-1800	DF	525	40	45.1	46.8	54.3	61.9	64.5	68.9	52.2	7	2	0.8400	23

¹ Based on cod catch per hour fished.

Catch quota regulations in force in 1975 for Subareas 2 and 3 are not sufficient to prevent continuing stock decline. A reduction in fishing effort of 30-40% may be necessary in Subareas 2 and 3 as a whole to even reduce fishing effort to the MSY level, especially since in both areas the fishing effort now on capelin is capable of being diverted back to groundfish with any improvement in catching prospects due to increased recruitment and/or availability.

Catch and Effort Trends for the Finfish Resources of the Scotian Shelf and Estimates of the Maximum Sustainable Yield of Groundfish (Except Silver Hake)

by

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ABSTRACT

Groundfish catches (excluding silver hake) from the Scotian Shelf (ICNAF Divisions 4VWX) reached a maximum of 322,000 metric tons in 1966, averaging 266,000 tons since then. Canada, Spain, USSR, and USA have been the major participants in the fishery. Using Canadian 151-500 GRT (gross registered tons) otter trawler catch and effort and total nominal catches, total effort was estimated for the period 1954-73. Estimated effort increased from 15,000 days fished in 1955-57 to 33,200 days by 1966, subsequently fluctuating around the 1966 level. Schaefer production models were fitted to these effort and catch per effort data and the effects of increasing fishing efficiency were examined. Estimates of maximum sustainable yield ranged from 230,000 tons to 280,000 tons. The best estimate from these data is 255,000 tons obtained from a model incorporating increases in fishing efficiency of 4% per year. This model predicts that a reduction in effort of 37% from the 1973 level is required to reduce effort to that giving maximum sustainable yield from these resources.

INTRODUCTION

This paper describes changes in nominal catches, fishing effort, and catch rates in Scotian Shelf fisheries (ICNAF Div. 4VWX) from 1954-73, but primarily from 1963-73. A simple general production model is applied to obtain a rough estimate of maximum sustainable yield for the groundfish resources as a whole, with the exception of silver hake.

Groundfish are defined liberally as all species other than silver hake, herring and mackerel, large pelagic species, and "inshore" species, i.e., eels, salmon, smelt, sturgeons, trouts, tomcod, alewife, shad and bass. This leaves, in addition to the "traditional" groundfish species (cod, haddock, redfish and flatfish), a variety of species which are normally caught in the offshore trawl fisheries. Silver hake, although a groundfish species, is treated separately because of the very large catches involved. Hence the term "groundfish" as used below, solely for convenience, excludes silver hake.

NOMINAL CATCHES

Groundfish catches from the Scotian Shelf were about 165,000 metric tons in 1954, the first year for which comprehensive statistics can be separated out for the Scotian Shelf in ICNAF Statistical Bulletins (Fig. 1). Other species catches in Subarea 4 cannot be allocated to the Scotian Shelf and Gulf of St. Lawrence prior to 1961. It is likely that total catch of all species from the Scotian Shelf was in the order of 200,000 tons in 1954. By 1961 the total catch was 291,500 tons (Table 1). (All statistics quoted here exclude large pelagic species and the small quantities of menhaden, butterfish and saury reported from Subarea 4.) From 1961, catches increased steadily to 773,000 tons by 1973.

¹ Submitted to 1975 Annual Meeting as Res.Doc. 75/43.

Groundfish catches reached a maximum of 322,000 tons in 1966 and have since averaged 266,000 tons. Catches in 1973 were 278,000 tons. Increasing total catches were maintained by expanded silver hake catches in 1963-64, then by increased herring catches from 1964 to 1969, and finally by a second large increase in silver hake catches from 1969 to 1973.

Cod has been the most important groundfish species in terms of volume (Table 1, Fig. 2). Cod catches averaged about 72,000 tons in 1954-58, then steadily increased to 131,700 tons by 1968. Subsequently catches have been lower, averaging 109,800 tons in 1969-73.

Table 1. Nominal catches from the Scotian Shelf (Div. 4VWX) by major species and species groups, 1961-73. (Data from ICNAF *Statistical Bulletin*, Vol. 11-23.)

Year	Cod	Haddock	Redfish	Flatfish	Pollock	Red and White hake
1961	98,498	45,253	31,484	12,255	29,352	3,428
1962	104,357	42,764	36,735	14,231	32,961	2,572
1963	113,288	49,929	38,759	16,007	30,471	2,622
1964	118,625	58,811	22,906	20,175	32,245	5,692
1965	126,457	84,087	19,578	30,283	27,729	10,026
1966	125,545	65,723	40,836	36,122	24,476	4,196
1967	101,321	48,101	18,259	26,020	14,787	2,147
1968	131,682	45,668	13,627	56,506	17,623	2,103
1969	98,980	41,566	22,993	34,194	15,221	3,814
1970	118,433	27,415	31,579	20,479	11,795	4,246
1971	105,318	30,918	62,381	38,054	12,072	6,806
1972	118,834	18,187	50,300	26,535	20,206	7,243
1973	107,605	17,494	40,173	31,482	30,100	7,526

Year	Cusk	Wolffish	Argentine	Skates	Angler	Other groundfish
1961	3,295	1,566	-	122	-	1,024
1962	3,695	1,391	-	111	-	5,079
1963	1,900	1,014	8,127	99	-	25,561
1964	4,367	1,152	4,943	1,271	96	8,446
1965	4,634	96	5,611	166	-	8,021
1966	4,997	130	14,983	51	696	4,227
1967	4,630	1,003	4,271	77	8	2,569
1968	3,154	1,655	2,675	6,290	2,428	4,629
1969	2,735	1,595	5,354	4,505	3,295	12,935
1970	3,216	103	4,553	3,910	2,123	11,531
1971	4,585	1,995	6,715	17,666	13,506	14,314
1972	5,300	1,405	5,868	5,265	2,879	9,688
1973	5,650	1,277	1,444	7,573	10,291	17,666

Year	Groundfish Subtotal	Silver hake	Herring	Mackerel	"Inshore" species	Total finfish ¹
1961	226,267	2	60,675	2,482	2,074	291,500
1962	243,896	8,854	79,116	4,438	2,053	338,357
1963	287,777	123,028	69,209	3,336	1,738	485,088
1964	278,729	81,147	95,010	4,728	1,444	461,058
1965	316,688	50,022	131,274	6,762	864	505,610
1966	321,982	10,323	192,037	7,397	1,345	533,084
1967	223,193	2,483	191,928	7,986	1,340	426,930
1968	288,040	3,547	250,320	15,312	1,680	558,899
1969	247,187	46,564	301,218	14,545	947	610,461
1970	239,383	169,045	245,645	14,256	1,052	669,381
1971	314,333	128,657	164,398	16,936	7,702	632,026
1972	271,710	114,048	192,046	13,045	5,524	596,373
1973	278,281	298,621	164,923	25,703	5,353	772,881

¹ Excluding large pelagics and small quantities of menhaden, butterfish and saury.

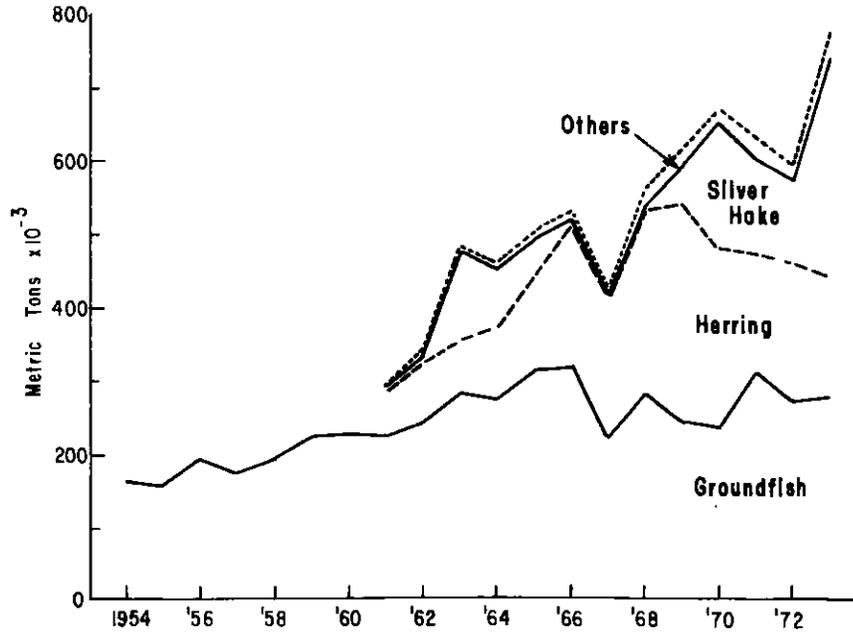


Fig. 1. Nominal catches of finfish by species or species group from the Scotian Shelf (ICNAF Div. 4VWX) 1954-73, excluding large pelagic species. ("Others" includes mackerel and inshore and diadromous species i.e. eels, salmon, smelt, sturgeons, trouts, tomcod, alewife, shad, bass, and also includes capelin. Successively higher lines represent cumulative totals. Data from ICNAF *Statistical Bulletin*, Vol. 4-23.)

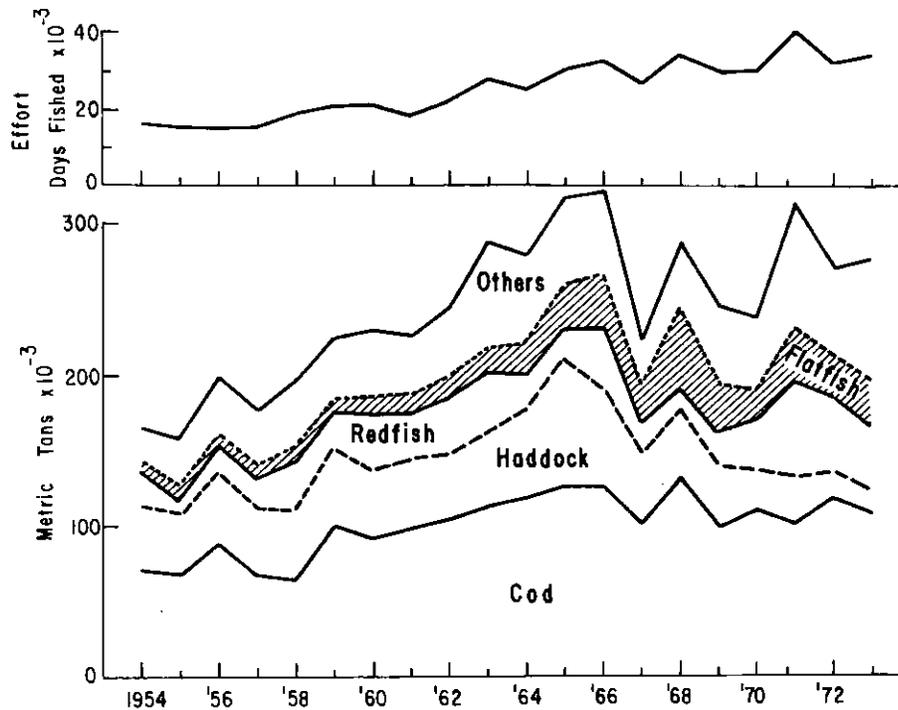


Fig. 2. Nominal catches of groundfish excluding silver hake by species from the Scotian Shelf (Div. 4VWX) 1954-73, and total fishing effort for groundfish in Canada (M) 151-500 GRT otter trawler units. (Successively higher lines in lower section represent cumulative totals. Data from ICNAF *Statistical Bulletin*, Vol. 4-23.)

In the 1950's and early 1960's haddock was the next most important species. Catches varied between 40,000 tons and 50,000 tons in 1954-63, but increased rapidly to 84,000 tons by 1965, then gradually declined to 17,500 tons by 1973. Flatfish catches increased from about 12,000 tons in 1961 to 56,500 tons in 1968, but averaged about 30,000 tons in 1969-73. In most recent years, redfish catches increased substantially to 60,000 tons in 1971 but declined to 40,000 tons by 1973, and pollock catches increased from 12,000 tons in 1971 to 30,000 tons in 1973. These increases, and increases in catches of less popular species, have sustained catches at an average of 266,000 tons.

CATCH RATES

Catch rates (metric tons per day fished) of all major tonnage classes of Canadian (Maritimes) vessels fishing groundfish have declined from 1964-65 to 1971 with apparent slight increases in most classes in 1972 and 1973 (Fig. 3). Separating major gear types within tonnage classes for vessels over 150 GRT indicates, however, that this recent increase is primarily a result of a change to midwater trawling for groundfish by a small proportion of vessels. The following catch rates (tons per day fished) were attained in 1971-73:

Year	151-500 GRT		501-900 GRT	
	Otter trawl	Midwater trawl	Otter trawl	Midwater trawl
1971	7.70	-	9.48	48.62
1972	8.39	30.21	10.30	36.27
1973	8.00	29.59	10.06	26.42

The catch rates of 501-900 GRT midwater trawlers declined by 46% between 1971 and 1973, whereas those of 151-500 GRT vessels and 501-900 GRT otter trawlers did not change significantly. (The catch rates of vessels smaller than 150 GRT have not been examined in detail.)

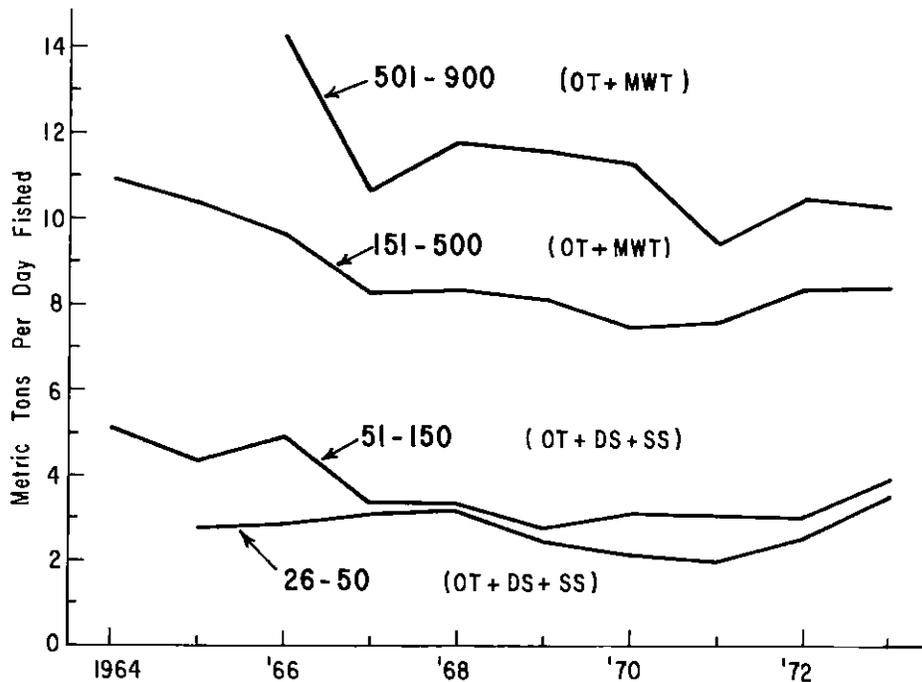


Fig. 3. Catch rates of all species (metric tons per day fished) by Canada (M) vessels on the Scotian Shelf (Div. 4VWX) 1964-73, by tonnage class. (OT = otter trawl, MWT = midwater trawl, SS = Scottish seine, DS = Danish seine.)

The catch rates of 501-900 GRT otter trawlers declined significantly from 19.48 tons per day fished (t/df) in 1965, when this class of vessel first entered the fishery, to 10.06 t/df in 1973 (Table 2, Fig. 4). The catch rates of 151-500 GRT otter trawlers were above 10.00 t/df between 1954 and 1965, the highest catch rate of 13.02 t/df being attained in 1956. Despite substantial vessel and gear improvements and the entry of a number of stern trawlers to this tonnage class (151-500 GRT), catch rates have gradually declined to 8.00 t/df in 1973.

Species composition of catches (Fig. 5) of 151-500 GRT otter trawlers (in terms of kg caught per hour fished which shows similar overall trends to t/df) in 1965-73 is very similar to the composition of total international catches in those years (Fig. 2). These vessels do not fish for silver hake, herring, or other pelagic species, or shellfish, but do fish for all of the major groundfish species.

Cod catch rates declined from 303 kg/hr in 1965 to 159 kg/hr in 1973, haddock from 190 kg/hr in 1966 to 69 kg/hr in 1973, flounders from 152 kg/hr in 1967 to 78 kg/hr in 1973. Redfish catch rates increased from 24 kg/hr in 1965 to 228 kg/hr in 1971, but declined to 155 kg/hr in 1973. Catch rates of other species, predominantly pollock, declined from 212 kg/hr in 1965 to 51 kg/hr in 1971, then increased to 168 kg/hr in 1973. Thus, there has been a succession of species forming important components of the catches as more desirable species declined in abundance, but this has not sustained overall catch rates which declined from 846 kg/hr in 1965 to 630 kg/hr in 1973.

Relatively few country x tonnage class x gear combinations have consistently fished the Scotian Shelf in the period 1963-73. Catch rates of those which did are summarized in Table 2 and Fig. 6. Catch rates of Canada (N) otter trawlers of 151-500 GRT declined from 13.71 t/df in 1965 to 10.13 t/df in 1973, and of 501-900 GRT otter trawlers from 19.23 t/df in 1966 to 12.24 t/df in 1973. France (M) otter trawlers of 901-1800 GRT had a catch rate of 32.47 t/df in 1964, but only 18.80 t/df in 1973. Spanish 151-500 GRT pair trawlers increased their catch rate to 22.35 t/df in 1968, but catch rates declined each year thereafter to 12.15 t/df in 1973. Spanish 901-1800 GRT otter trawler catch rates declined between 1964 and 1968, increased substantially in 1969, then declined to 1972. USA 151-500 GRT otter trawlers suffered declining catch rates between 1966 and 1969, but returned to the 1966 level by 1972, declining slightly in 1973. All of these vessel classes have fished "traditional" groundfish species. Declines in French and Spanish catch rates largely reflect declining cod abundance. Recent increases in USA catch rates reflect the importance of redfish which increased in abundance in the early 1970's.

Catch rates of USSR >1800 GRT trawlers are unique among these data sets in having highest catch rates in most recent years, the highest (44.31 t/df) occurring in 1973. USSR nominal catches (Fig. 7), which were predominantly by this vessel class, have been dominated by silver hake and recent increases in catch rates reflect high silver hake abundance. High abundance of traditional groundfish, particularly haddock, produced the 1965 peak in catch rates. Very low silver hake abundance in 1967 was not reflected by low catch rates but by diversion of effort from the area.

Table 2. Catch rates (metric tons per day fished) for major vessel categories fishing the Scotian Shelf (Div. 4VWX), 1963-73. (Data derived from ICNAF *Statistical Bulletin*, Vol. 13-23. Parentheses indicate values based on very small amounts of effort. OT = otter trawl; PT = pair trawl.)

Year	Canada(M)		Canada(N)		France(M)	Spain		USSR	USA
	151-500	501-900	151-500	501-900	901-1800	151-500	901-1800	>1800	151-500
	OT	OT	OT	OT	OT	PT	PT	OT	OT
1963	10.19	-	12.13	-	25.00	15.49	30.36	36.45	14.66
1964	10.95	-	12.49	-	32.47	16.66	34.67	35.54	13.03
1965	10.40	19.48	13.71	15.45	28.88	19.16	20.64	40.60	14.83
1966	9.71	14.41	12.86	19.23	32.11	17.01	(5.00)	33.41	21.83
1967	8.28	10.69	12.70	15.27	30.33	14.83	18.42	33.65	11.98
1968	8.34	11.84	12.69	15.92	(16.22)	22.35	16.04	39.41	12.32
1969	8.23	11.63	12.18	13.88	(29.75)	17.64	36.24	42.59	8.03
1970	7.68	11.38	10.58	13.22	24.97	17.39	31.74	41.06	9.30
1971	7.70	9.48	11.18	11.96	20.60	15.04	22.75	36.40	15.23
1972	8.39	10.30	11.25	15.61	18.21	13.37	13.81	37.32	22.07
1973	8.00	10.06	10.13	12.24	18.80	12.15	16.12	44.31	19.89

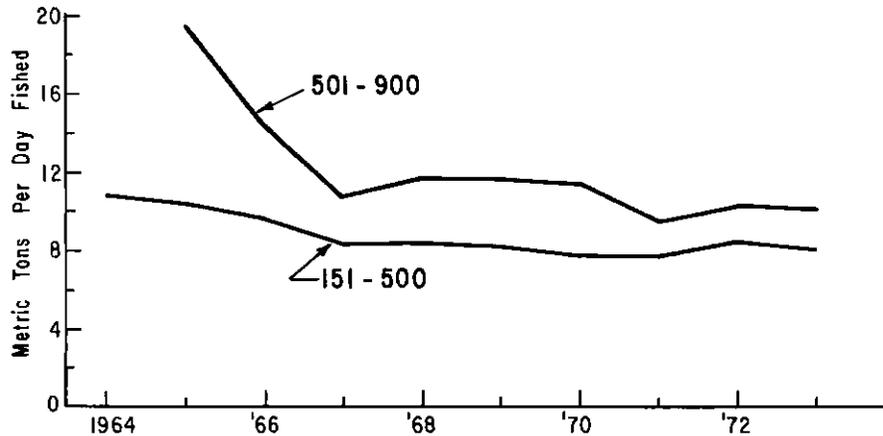


Fig. 4. Catch rates of all species (metric tons per day fished) by Canada (M) bottom otter trawlers of 151-500 gross tons and 501-900 gross tons on the Scotian Shelf (Div. 4VWX) 1964-73.

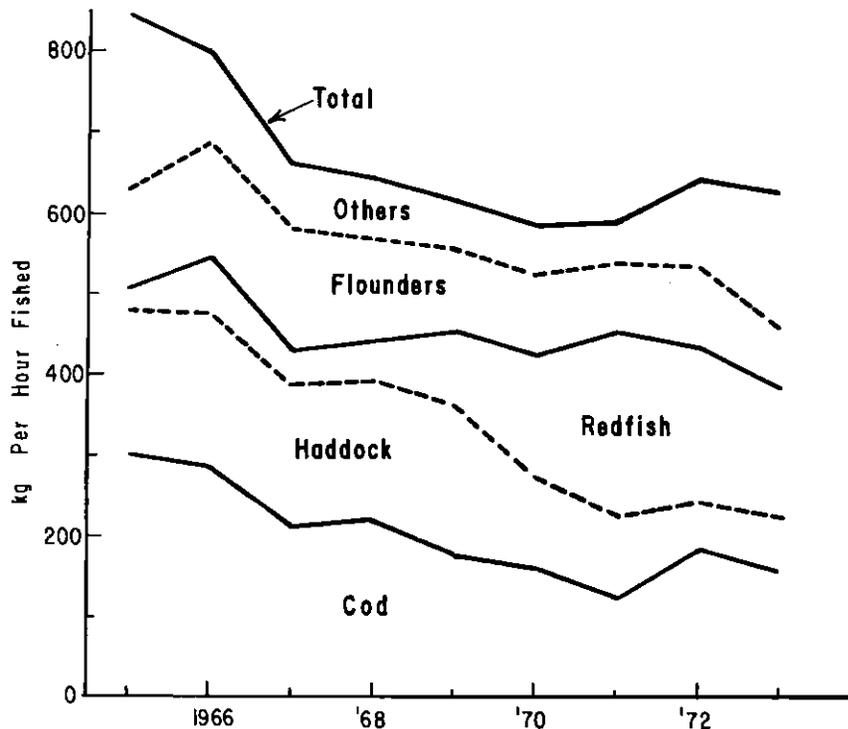


Fig. 5. Catch rates by species (kg. per hour fished) of Canada (M) bottom otter trawlers of 151-500 gross tons on the Scotian Shelf (Div. 4VWX) 1965-73.

Catch rates for Canadian vessels (only) in 1974 became available to the authors subsequent to completion of the following analysis. Canada (M) 151-500 GRT otter trawler catch rates declined 11% to 7.12 t/df in 1974 from 8.00 t/df in 1973. Canada (M) 501-900 GRT otter trawler catch rates declined 13% to 8.80 t/df in 1974 from 10.06 t/df in 1973. Preliminary data for these vessel classes for the first six months of 1975 indicate that further declines took place over the same period in 1974. In January to June 1974, catch rates of 151-500 GRT vessels were 7.65 t/df, whereas in the same period in 1975 catch rates were 7.63 t/df. For 501-900 GRT vessels in the same period catch rates were 9.61 t/df in 1974 and 9.33 t/df in 1975. Thus, declines in catch rates continued through 1974 and may well continue through 1975.

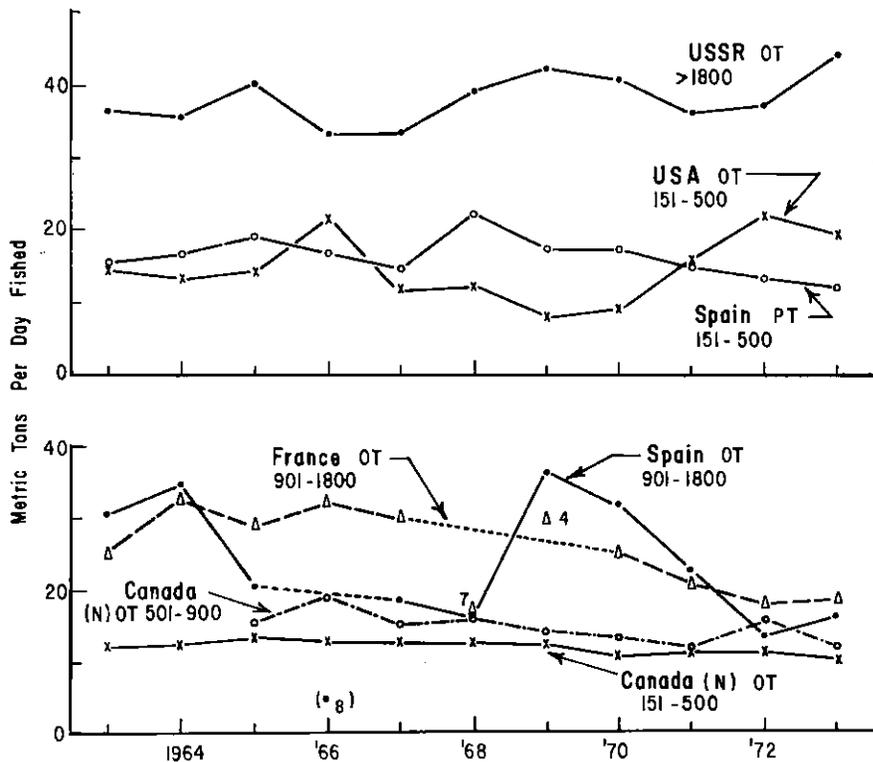


Fig. 6. Catches rates of all species for important Country x gear x tonnage categories fishing the Scotian Shelf (Div. 4VWX) 1963-73. (OT = otter trawl, PT = pair trawl. Data points for Spanish OT 901-1800 GRT for 1966 and for French OT 901-1800 GRT for 1968 and 1969 are not included in trend lines as they are based on less than 10 days fished.)

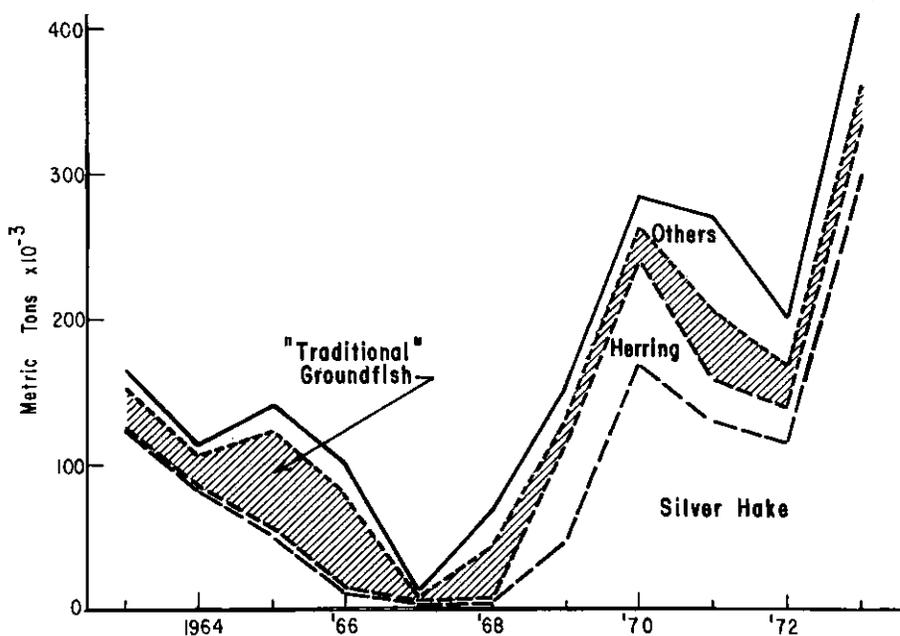


Fig. 7. USSR nominal catches of finfish from the Scotian Shelf (Div. 4VWX) 1963-73. ("Traditional groundfish" = cod, haddock, redfish and flatfish.)

EFFORT

Canada, Spain, USSR, and USA have consistently exerted substantial effort on the Scotian Shelf, although USA effort dropped below 1,000 fishing days after 1967. The full record of effort is available in ICNAF Statistical Bulletins. Effort on the Scotian Shelf in 1973 is presented here, as an example (Table 3).

As discussed above, Canada (M) otter trawlers of 151-500 GRT has been the most consistent effort class, exerting a high volume of effort throughout the recorded data series from 1954 to 1973. They have also fished all the major groundfish species throughout this period. The vessels involved have changed, with substantial improvements in gear and design including introduction of some stern trawlers to this class. These changes will have tended to minimize the observed decline in catch rates over the time period. This vessel class has been chosen to investigate total effort trends in the groundfish fisheries, estimates of total groundfish effort being obtained by dividing total catch by Canada (M) 151-500 GRT otter trawler catch per unit effort. These estimates indicate that effort increased steadily from 1957 to 1966 (Fig. 2). In 1955-57, about 15,000 days were fished with effort increasing (with small fluctuations) to 33,200 days in 1966. Effort has fluctuated between about 27,000 and 41,000 days since 1966, with an average close to the 1966 level. The 1973 effort level was 34,800 days.

MAXIMUM SUSTAINABLE YIELD OF GROUNDFISH

The maximum sustainable yield and current status of Scotian Shelf groundfish resources were examined by application of the Schaefer production model to catch rates of Canada (M) 151-500 GRT otter trawlers and the standardized effort derived from them (Table 4).

Examination of catch per effort (C/E) in relation to time indicated a downward trend with decreasing variance. A regression line of $\log(C/E)$ against year has the form (r = correlation coefficient):

$$\log(C/E) = 1.594 - 0.0095(\text{YEAR}) \quad (r = -0.83)$$

A plot of residuals revealed positive correlations in successive residuals. Therefore, a first order autoregressive model was considered. The resulting equation is, for year t :

$$\log(C/E)_t = 1.0624 + 0.3807 \log(46(t-1)) - 0.00707t \quad (r = -0.89)$$

These regressions, taken together, indicate that a consistent decline in C/E began in 1954 so that the population fished was never in equilibrium from 1954 to 1973. Therefore, the equilibrium C/E must be less than that suggested by these data.

Gulland's (1968) method, plotting C/E against effort averaged over a number of preceding years, was used to correct for the non-equilibrium conditions in the fishery. The correlation between C/E and effort increases with increases in the averaging period for effort up to three years ($r = -0.88$), declines with four years, but again increases progressively up to seven years ($r = -0.92$). It is unlikely that the time lag in population response to fishing is greater than seven years. Thus, longer averaging periods were not considered.

The regression line of C/E on three-year running averages of effort and the resultant equilibrium catch curve implies that maximum equilibrium catch is 280,000 tons attained with an effort of 37,500 days (Fig. 8). Effort exceeded this level only in 1971 (Fig. 9). The seven-year averaging period gives an estimated MSY of 253,000 tons attained with an effort of 32,500 days, a level exceeded in the four years 1966, 1968, 1971 and 1973.

As noted above, substantial increases in efficiency of this vessel class have occurred in the 1954-73 period, due to increases in the size and power of vessels, improvements in gear and navigational and acoustic equipment, and improvements in vessel design including introduction of some stern trawlers to the class. To allow for these changes, a steady rate of increase in efficiency was introduced into the model. Running averages of effort were varied from three to seven years and increases in efficiency varied from one to five percent per year. The highest correlation between C/E and effort was obtained using five-year running averages and four percent increase in efficiency ($r = -0.97$). This suggests that the MSY is 255,000 tons (Fig. 10) and that effort exceeded that required to obtain this catch level in 1966 and from 1968 to 1973 inclusive.

Table 4. Catch rates of Canadian otter trawlers of 151-500 GRT, 1954-73, and estimated total effort for groundfish (excluding silver hake) on the Scotian Shelf (Div. 4VWX).

Year	Tons per day fished	Effort (days)	Year	Tons per day fished	Effort (days)
1954	10.22	16,134	1964	10.95	25,455
1955	10.54	14,973	1965	10.40	30,451
1956	13.02	15,123	1966	9.71	33,160
1957	11.47	15,475	1967	8.28	26,957
1958	10.32	19,001	1968	8.37	34,413
1959	10.53	21,393	1969	8.23	30,035
1960	10.56	21,767	1970	7.68	31,170
1961	11.98	18,887	1971	7.70	40,822
1962	10.91	22,355	1972	8.39	32,385
1963	10.19	28,241	1973	8.00	34,785

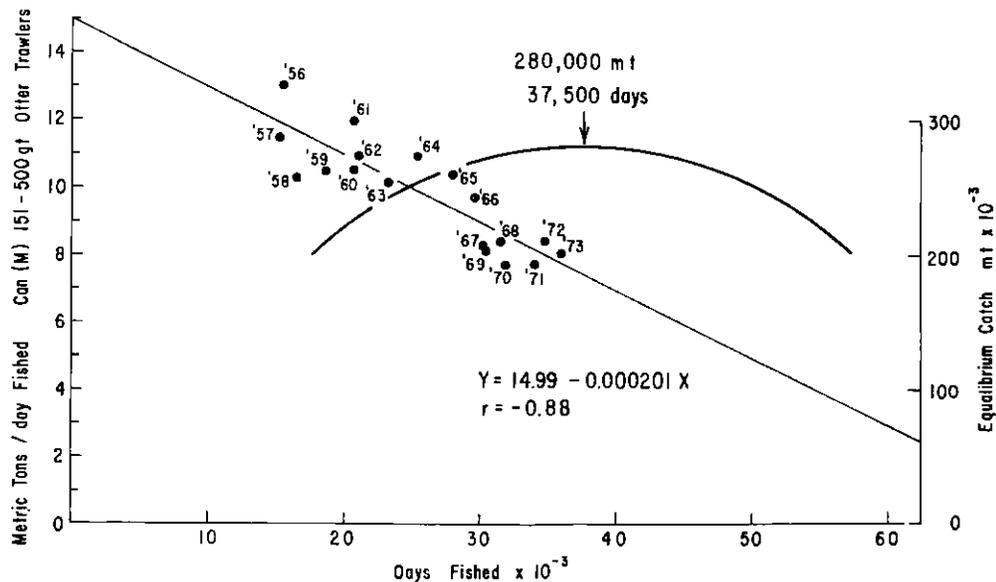


Fig. 8. Regression of catch rates on (3 year running average of) effort and resultant equilibrium yield curve for groundfish (excluding silver hake) on the Scotian Shelf (Div. 4VWX). (Standardised days fished calculated by dividing total catch by catch per day (metric tons) of Canada (M) 151-500 gross ton otter trawlers.)

Walter (MS 1975) proposed an alternative method to that of Gulland to correct for non-equilibrium in the fishery. Following Walter, a first approximation to the relationship of C/E and effort was obtained by plotting C/E in year t+1 against effort in year t. An adjustment for efficiency increase of 4% per year also gave the best fit in this analysis. The least squares regression line

$$C/E = 11.64 - 0.000120 (\text{Effort}) \quad (r = -0.92)$$

suggests an MSY of 282,000 tons at an effort approximately equal to the 1965 value. Effort in 1966 and in 1968-72 substantially exceeded this level.

An attempt to obtain a second approximation using Walter's method of plotting $\Delta U/U$ versus $11.64 - U - 0.000120F$ (where $U = C/E$ and $F = \text{effort}$) did not yield a significant regression, and hence little reliance could be placed on corrected C/E values. Continuing the calculation, despite this, yielded a second approximation to the MSY of about 230,000 tons.

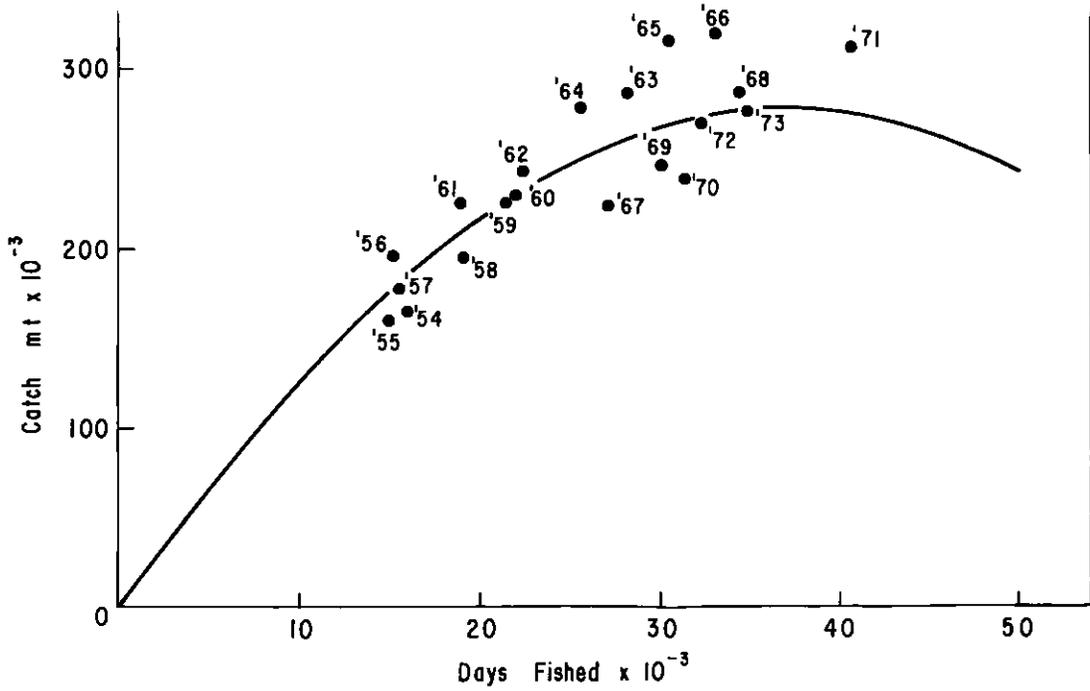


Fig. 9. Plot of catches against effort for groundfish (excluding silver hake) on the Scotian Shelf (Div. 4VWX), 1954-73, and equilibrium yield curve from Fig. 8.

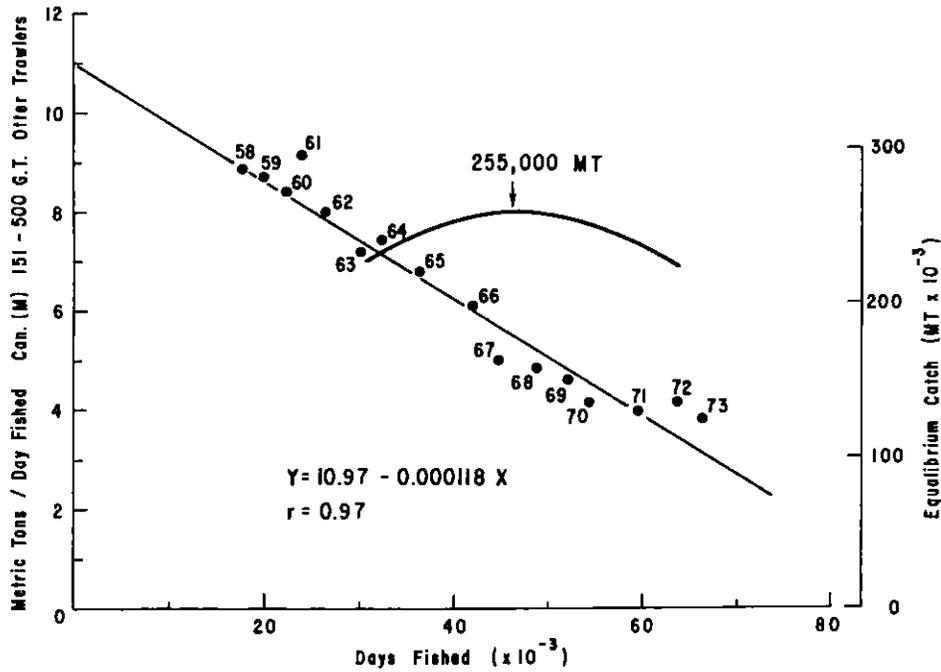


Fig. 10. Regression of catch rates on effort and resultant equilibrium yield curve for groundfish (excluding silver hake) on the Scotian Shelf (Div. 4VWX). A five year running average of effort is used and the data are corrected for a constant increase in efficiency of 4% per year.

CONCLUSIONS

Application of the Schaefer production model to catch and effort data for the Scotian Shelf groundfish resources (excluding silver hake) from 1954 to 1973 indicates that their MSY is unlikely to be greater than 280,000 tons and could be as low as 230,000 tons. Recent levels of effort are at least sufficiently high to attain this yield, but could in fact be 40% to 50% above this level.

Groundfish species catch quotas for Scotian Shelf stocks set for 1975 sum to 242,000 tons. This assumes that 50% (25,000 tons) of the TAC for cod in Subdiv. 4Vn(Jan-Apr) + Div. 4T and about 70% (40,000 tons) of the TAC for pollock in Div. 4VWX + Subarea 5 are taken on the Scotian Shelf, i.e., that the proportions remain the same as in 1972 and 1973. Additional catches will be taken of unregulated species stocks, catches of which averaged 58,000 tons in the four-year period 1970-73. Thus, if all catch quotas are taken in 1975 and if non-regulated species catches are at recent levels, the total catch would be 300,000 tons.

Some increase in vessel efficiency has certainly occurred and the time lag in population response to fishing can be expected to be greater than three years (if the primary response is through the recruitment mechanism), since the primary species (cod, haddock, redfish and flounders) do not mature until age 4 or older. Thus, it is likely that the MSY is substantially below 280,000 tons, and that recent levels of effort have resulted in over-exploitation. This is substantiated by the fact that average catches of 278,000 tons over the last 10 years have resulted in continuing stock decline.

Catch quota regulations in force in 1974 and 1975 are not sufficient to prevent continuing stock decline. The reduction in effective effort below the 1973 level required to obtain MSY could be as much as 50%. If the results of the Schaefer model using five-year running averages of effort and a 4% efficiency increase are accepted, the reduction in effort required from the 1973 level is 37%.

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Non-equilibrium Regulation of Fisheries¹

by

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INTRODUCTION

Many of the world's fisheries have until recently been in a virgin state or close to it. The exploitation has been marginal and has not severely affected the stock size. In the last twenty years these fisheries have come under increasing exploitation, which has often reduced the stock size and necessitated some sort of regulation of the catch.

There are many theories available to the fisheries biologist for this regulation. They usually give an estimate for the maximum yield that the fishery can produce on a continuing basis, i.e. the maximum sustained yield (MSY). It should be observed that this value is not the maximum possible catch in a given year but, particularly in a virgin fishery, is considerably less.

The newly exploited stock is usually difficult to manage. Few data are available and they are often unreliable. Moreover, the stock is not in equilibrium in the presence of fishing. This latter fact is often overlooked and is one of the reasons for the shrinking estimates of MSY that are sometimes encountered.

In this work we shall study the yield of a fishery under nonequilibrium conditions and compare strategies for bringing the stock size to that required for maximum sustained yield. We shall consider reduction to this optimum stock size from above as well as increase from below.

We introduce a procedure based on the equation of Schaefer which assumes the growth rate of the total stock biomass to be a function of the biomass itself and of fishing effort. Although no delayed effects are present in the equation, we shall see that there is considerable delay between the initiation of a regulation and the attainment of the desired equilibrium state.

MATHEMATICAL FORMULATION

The equation of Schaefer (1954) is:

$$\frac{1}{P} \frac{dP}{dt} = r \left(1 - \frac{P}{P_{\infty}}\right) - qf \quad (1)$$

where P represents the biomass of the stock in question, f the fishing effort, r is the maximum instantaneous growth rate of the stock, P_{∞} is the equilibrium biomass in the absence of fishing, and q is the coefficient of catchability. Under conditions of equilibrium the rate of growth is zero and the equation becomes:

$$0 = r \left(1 - \frac{P_e}{P_{\infty}}\right) - qf \quad (2)$$

where P_e is the equilibrium biomass. The equilibrium yield is given by:

$$y_e = qfP_e = qf \frac{P_{\infty}}{r} (r - qf). \quad (3)$$

The maximum value of the equilibrium yield is attained when $f = \frac{r}{2q}$ and is given by:

$$y_e (\max) = \frac{r}{4} P_{\infty}. \quad (4)$$

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As Schaefer observed but did not exploit in his yield equation, few fisheries are in a state of equilibrium. It could further be added that most are in a state of decline (Edwards and Hennemuth, 1975). Thus it seems desirable to calculate the yield under non-equilibrium conditions. We must introduce a time variable in order to make this calculation. Accordingly, let y_n be the yield of a fishery during the course of the n^{th} year of fishing at the constant effort, f . We assume that the stock biomass satisfies equation (1). Then we see that:

$$y_n = \int_{n-1}^n qfP dt = qf \int_{n-1}^n P dt, \quad (5)$$

from which, by solving (1) for P and substituting the answer in (5), we obtain:

$$\begin{aligned} y_n &= qf \int_{n-1}^n P_{\infty} \left(1 - \frac{dP/dt}{rP} - \frac{qf}{r}\right) dt \\ &= qfP_{\infty} - \frac{qfP_{\infty}}{r} \cdot \ln(P) \int_{n-1}^n \frac{-q^2 f^2 P_{\infty}}{r} \\ &= \frac{qfP_{\infty}}{r} (r - qf) + \frac{qfP_{\infty}}{r} \cdot \ln \left(\frac{P_{n-1}}{P_n} \right). \end{aligned} \quad (6)$$

Here P_{n-1} denotes the biomass at the beginning and P_n at the end of the n^{th} year. The first term in the last expression may be observed to be, by comparison to (3), the yield under equilibrium conditions for the year. Thus (6) may be expressed as:

$$y_n = y_e + \frac{qfP_{\infty}}{r} \cdot \ln \left(\frac{P_{n-1}}{P_n} \right) \quad (7)$$

where the second term on the right represents the yield resulting from changes in the biomass. It will be either positive or negative depending on whether P_{n-1} is greater or less than P_n . Of course P_n cannot be set arbitrarily but depends on P_{n-1} and on f . We may calculate the value of P_n by solving (1) for P with the initial value P_{n-1} . This solution is given by:

$$P_n = (P_{n-1}) \cdot \frac{r - qf)P_{\infty}}{rP_{n-1} - (rP_{n-1} - (r-qf)P_{\infty}) - \exp(-(r-qf))}. \quad (8)$$

This expression may be simplified somewhat. The level of fishing effort f_{∞} beyond which the population will be annihilated eventually is given by:

$$f_{\infty} = \frac{r}{q}.$$

We denote by x that fraction of this effort that corresponds to f , i.e.:

$$x = f/f_{\infty}.$$

Then (8) becomes, in terms of x :

$$P_n = \frac{P_{n-1} (1-x)P_{\infty}}{P_{n-1} - (P_{n-1} - (1-x)P_{\infty}) \cdot \exp(-(1-x)r)}. \quad (9)$$

In considering the virgin initial state, we take $n-1$ equal to 0 and set P_0 equal to P_{∞} . In this case (9) reduces to:

$$P_1 = \frac{(1-x)P_{\infty}}{(1-x) \cdot \exp(-(1-x)r)}. \quad (10)$$

This may be substituted into (6) and f replaced by $\frac{xr}{q}$ to obtain the expression:

$$y_1 = xP_{\infty}(1-x)r + xP_{\infty} \cdot \ln \left(\frac{1 - xe^{-(1-x)r}}{1-x} \right) \quad (11)$$

for the yield of a virgin fishery during the first year of exploitation. It has the same general form as the equilibrium yield curve except that the maximum occurs at different values of x (of f). Figure 1 is a plot of both curves for $r = 0.2$. If r is small compared to 1, then the exponential function in (11) may be approximated by the first two terms of its power series. The simplified version is then:

$$y_1 \approx rP_{\infty}x(1-x) + xP_{\infty} \cdot \ln(1+rx) \quad (12)$$

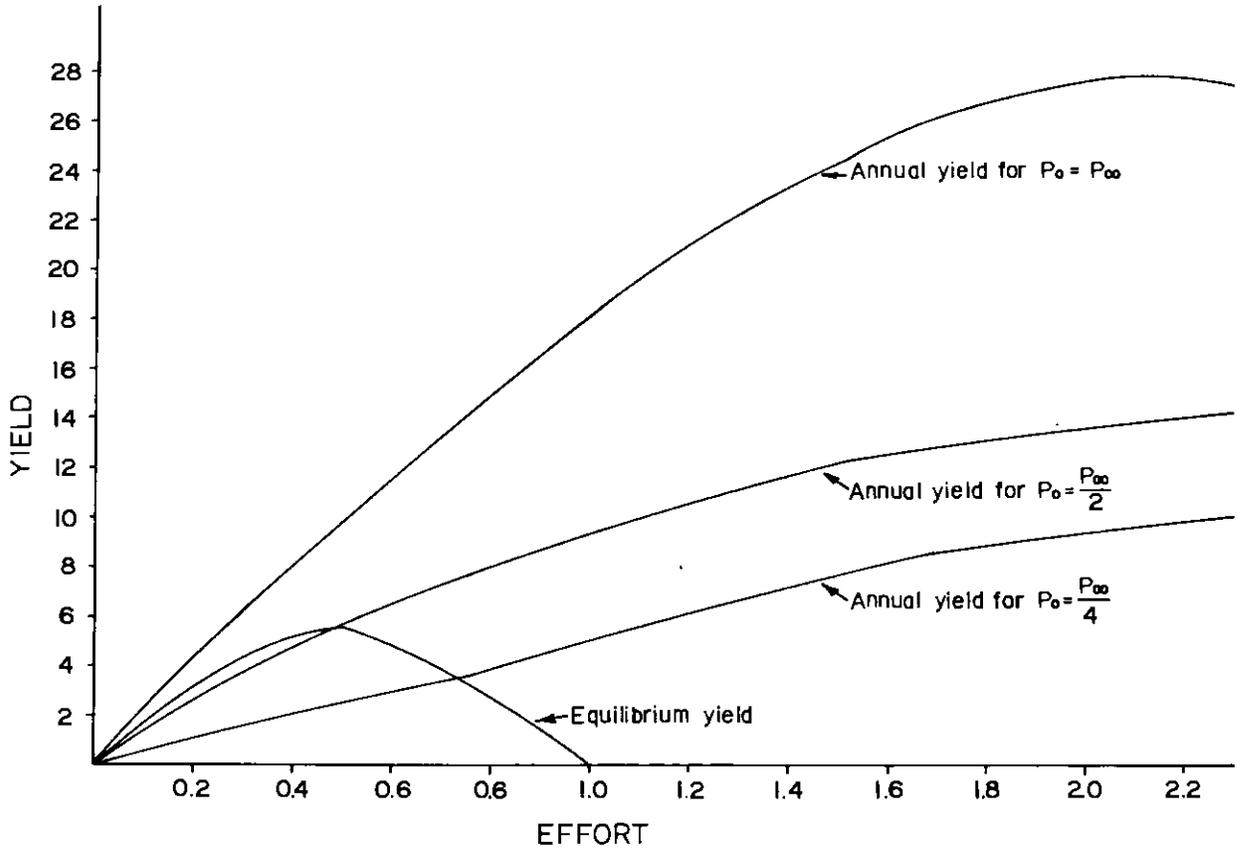


Fig. 1. Annual yields and equilibrium yield for a hypothetical fishery with $P_{\infty} = 100$ and intrinsic growth rate $r = 0.2$. Annual yield is calculated for an initial population biomass to P_{∞} , $P_{\infty}/2$, and $P_{\infty}/4$.

TWO POSSIBLE STRATEGIES

The strategy of choosing that f which maximizes the yield is clearly inadequate in the nonequilibrium case. Indeed, as a reference to Fig. 1 shows, the value of x which would maximize yield in the first year would be greater than any which could be sustained.

The simplest strategy to use is the constant effort, set at the level that would give maximum sustained yield, i.e. at $x = \frac{1}{2}$. The yield in this case will decrease asymptotically to the maximum sustainable yield. During the first year the yield will be:

$$Y_1 = Y_e + \frac{P_{\infty}}{2} \cdot \ln(2 - e^{-r/2})$$

during the second,

$$Y_2 = Y_e + \frac{P_{\infty}}{2} \cdot \ln\left(\frac{2 - e^{-r}}{2 - e^{-r/2}}\right)$$

and during the n^{th} ,

$$Y_n = Y_e + \frac{P_{\infty}}{2} \cdot \ln\left(\frac{2 - e^{-nr/2}}{2 - e^{-(n-1)r/2}}\right). \quad (13)$$

Thus the yield would be gradually decreasing from a first year which is almost double the maximum sustained yield for small values of r to one which approaches it as n increases.

An alternative strategy to the constant effort would be one in which the yield is constant in each year at the MSY level. In this case the effort would increase gradually to that necessary for maximum sustained yield. The effort required in the first year may be calculated by first setting y_1 in equation (11) to the MSY and then solving it for x . The usual approximations lead to the equation

$$1 + r\left(\frac{1}{4x} - 1 + x\right) = 1 + rx \quad (14)$$

which when solved for x yields:

$$x_1 = \frac{1}{4},$$

the approximate effort needed for a first year yield equal to the MSY. In order to calculate the level of effort for subsequent years, we use equation (9), approximate the exponential function by a linear function and after some simplification find that:

$$\frac{P_{n-1}}{P_n} = r\left(\frac{P_{n-1}}{P_\infty}\right) - 1 + 1 + rx \quad (15)$$

and hence that the yield during the n^{th} year is approximately

$$y_n = xP_\infty(1-x)r + xP_\infty \cdot \ln\left[r\left(\frac{P_{n-1}}{P_\infty} - 1\right) + 1 + rx\right]. \quad (16)$$

This may be set equal to $rP_\infty/4$ as was done in the previous case and solved for x_n to obtain:

$$x_n = \frac{P_\infty}{4P_{n-1}}. \quad (17)$$

From equation (15) it follows that P_n/P_{n-1} is always less than 1 for P_{n-1} between $P_\infty/2$ and P_∞ , and hence P_n is monotonically decreasing to $P_\infty/2$ as x_n approaches $1/2$.

Either of these strategies is successful if the correct values of f_{MSY} and MSY are known. The constant yield strategy would be easiest to regulate through catch quotas and the constant effort through effort regulation, although by using our calculations either regulation is possible in each case. The constant effort strategy reduces the biomass to maximum production more rapidly than the constant yield strategy. Figure 2 shows the successive operating points for both.

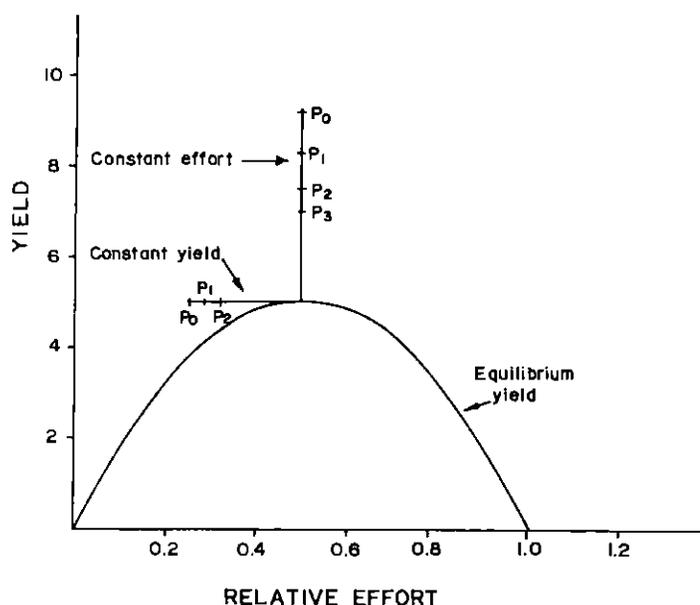


Fig. 2. Two strategies for reducing a virgin state fishery to the optimum level of biomass. Parameters are $P_\infty = 100$ and $r = 0.2$.

Unfortunately, for most fisheries, the values of f_{MSY} and MSY are known only approximately, particularly in the early years of a heavily exploited fishery when the need for regulation becomes apparent. Accordingly we shall investigate the effect of errors in estimation on the strategies.

EFFECT OF ERRORS IN THE ESTIMATES

Let us first suppose that the maximum sustained yield is underestimated by an amount ϵP_∞ but that the corresponding effort is known exactly. The effect on the constant effort strategy would be nil if the fishing were regulated through effort. The effect on the constant yield strategy regulated through catch quotas would be to stabilize the fishery at the levels:

$$\hat{Y}_e = \frac{rP_\infty}{4} - \epsilon P_\infty, \quad (18)$$

$$\hat{x}_e = \frac{1}{2} - \sqrt{\epsilon/r}. \quad (19)$$

which would lead to under-utilization of the fishery through underfishing, but which could be corrected in subsequent years.

If the MSY were overestimated by an amount ϵP_∞ the constant effort strategy again would be unaffected. For the constant yield case, the biomass during the n th year, by equation (16) would satisfy:

$$\frac{rP_\infty}{4} + \epsilon P_\infty = xP_\infty(1-x)r + xP_\infty \ln \left[r(P_{n-1}/P_\infty - 1) + 1 + rx \right]. \quad (20)$$

This may again be solved for the necessary relative effort x which is

$$x_n = \frac{P_\infty}{4P_{n-1}} \cdot \left(1 + \frac{4\epsilon}{r} \right), \quad (21)$$

and which may be substituted into equation (15) to obtain

$$\frac{P_{n-1}}{P_n} = r \left(\frac{P_{n-1}}{P_\infty} \right) - 1 + \frac{rP_\infty}{4P_{n-1}} + \frac{\epsilon P_\infty}{P_{n-1}} + 1. \quad (22)$$

By letting $n = 1$ and setting $P_0 = P_\infty$, we obtain:

$$P_1 = P_\infty \left(\frac{4}{4\epsilon + 4 + r} \right) \leq \frac{P_\infty}{(1+\epsilon)}.$$

To find the limit as $n \rightarrow \infty$, we use the fact that for any real number $a > 0$,

$$a + \frac{1}{4a} - 1 \geq 0.$$

By setting $a = P_{n-1}/P_\infty$ we see that

$$r \left(\frac{P_{n-1}}{P_\infty} - 1 \right) + \frac{rP_\infty}{4P_{n-1}} \geq 0$$

and hence that

$$\frac{P_{n-1}}{P_n} \geq 1 + \frac{\epsilon P_\infty}{P_{n-1}} \geq 0. \quad (23)$$

Thus the sequence (P_n) satisfies the inequality

$$P_n \leq P_\infty (1 + \epsilon)^{-n} \quad (24)$$

which in the limit is

$$\lim_{n \rightarrow \infty} (P_n) = 0.$$

Hence this strategy can reduce the biomass to very low levels if not corrected. For example, if the MSY is overestimated by 10%, the biomass will decline to 10% of its equilibrium value in less than 24 years, by equation (24). If the MSY is overestimated by 25%, the decline will take less than 10 years.

We now turn to the question of error in the estimation of f_{MSY} . Suppose it is assumed to occur at:

$$\hat{x} = \frac{1 \pm \delta}{2},$$

and the fishery regulated accordingly. Under the constant yield strategy, this error will have no effect if the fishery is regulated by catch. Under the constant effort strategy, the yield will stabilize at something less than the optimum level. Indeed, from equation (11) we may calculate that the equilibrium level attained will be:

$$\begin{aligned} \hat{y}_e &= rP_\infty \left(\frac{1 \pm \delta}{2} \right) \cdot \left(1 - \left(\frac{1 \pm \delta}{2} \right) \right) \\ &= rP_\infty \left(\frac{1}{4} - \frac{\delta^2}{4} \right). \end{aligned} \quad (25)$$

Thus an error of 100% percent in estimating the optimum effort leads to an error of $(10\delta)^2$ percent in the yield. For example an error of 50% in the estimate will lead to a reduction in the ultimate equilibrium yield of 25%.

The effect of small errors in the estimates of MSY and corresponding effort generally are not fatal except in the case (see Fig. 3) of overestimation of MSY in a fishery regulated by catch in which the constant yield strategy is followed. It is of interest to investigate the nature of appropriate corrective action.

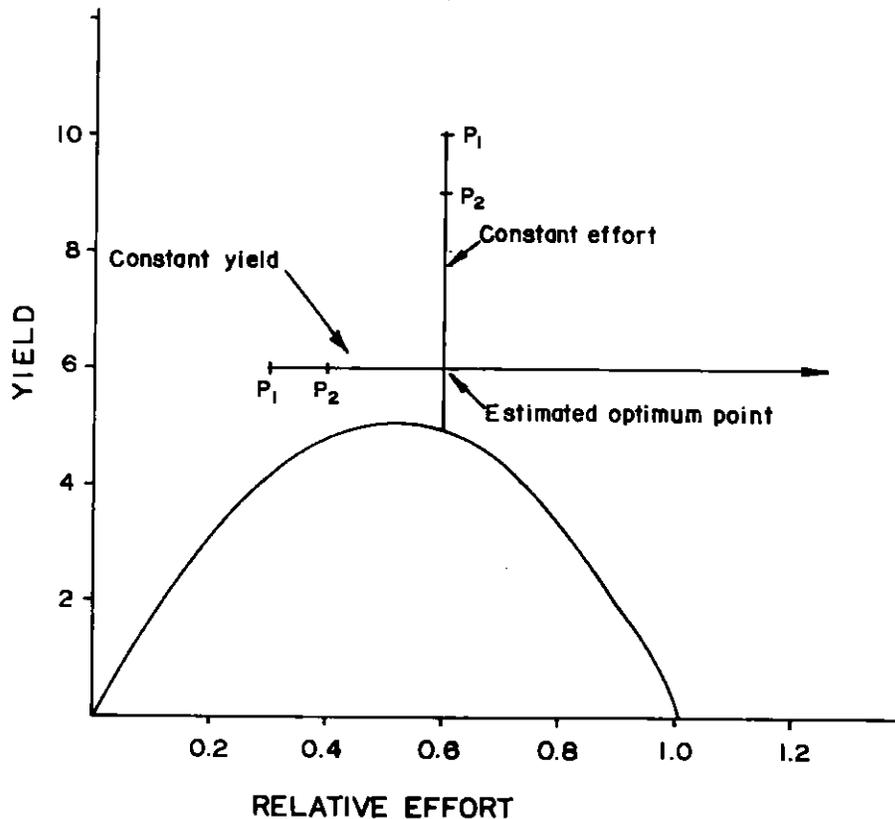


Fig. 3. The effect of overestimating MSY and optimum effort on constant yield and constant effort strategy for a hypothetical fishery with $P_\infty = 100$ and $r = 0.2$.

CORRECTIVE STRATEGY FOR INITIAL ERRORS

Let us suppose that initially the MSY is overestimated by an amount $\varepsilon_1 P_\infty$. After n_1 years the error is discovered and the regulation changed to account for the initial error. What the new allowable catch should be depends on n_1 and the initial error.

The choice of setting the maximum catch at the new estimate for the MSY is a bad strategy whenever the biomass has been reduced by more than half from the virgin level. It would lead to continued reduction of the biomass if the actual catch approaches the allowed maximum. The reason for this is that the effort would be:

$$x_{n_1} = \left(\frac{P_\infty}{4P_{n_1}} - 1 \right) \cdot \left(1 - \frac{4\varepsilon}{r} \right) > \frac{1}{2} \left(1 + \frac{4\varepsilon}{r} \right), \quad (26)$$

which is greater than the optimum value of $\frac{1}{2}$. By repeating the argument which led to equation (24), we can deduce that

$$P_n \leq \left(\frac{1}{rB+1} \right)^{n-n_1} \cdot (P_{n_1} - 1), \quad (27)$$

where

$$B = \left(\frac{P_{n_1-1}}{P_\infty} - 1 + \frac{P_\infty}{4P_{n_1-1}} \right).$$

Thus a catch at the MSY level will lead to a continued reduction in the biomass.

Clearly, some other corrective action must be taken. One possibility is to switch to effort regulation which, if the estimate of f_{MSY} is not greatly in error, will lead to recovery of the stock. Another is to set the catch at the level which would correspond to the optimum effort.

This catch would be below the MSY as is clarified by Fig. 4. The appropriate catch level, by equation (16) with $x = \frac{1}{2}$, is:

$$y = \frac{rP_\infty}{4} + \frac{P_\infty}{2} \cdot \ln \left(r \left(\frac{P_{n-1}}{P_\infty} - \frac{1}{2} \right) + 1 \right) \quad (28)$$

which, since P_{n-1}/P_∞ is less than $\frac{1}{2}$, is less than the MSY ($rP_\infty/4$). This may be further approximated by replacing the \ln function by the first two terms of its power series to obtain:

$$y \approx \frac{rP_\infty}{4} + \frac{P_\infty}{2} \left(\frac{rP_{n-1}}{P_\infty} - \frac{r}{2} \right) = \frac{rP_{n-1}}{2}. \quad (29)$$

The yield in year $n-1$ in turn may be obtained from equation (5) by approximating the average biomass (given by the integral) by the biomass at the end of that year:

$$Y_{n-1} \approx qf_{n-1} \cdot P_{n-1}. \quad (30)$$

Here f_{n-1} denotes the effort in year $n-1$. This in turn may be solved for P_{n-1} and substitutes in equation (29) to obtain

$$Y_n \approx \frac{ry_{n-1}}{2qf_{n-1}} = \frac{Y_{n-1}}{f_{n-1}} \cdot f_{opt} \quad (31)$$

since $f_{MSY} = 4/(2q)$. This formula gives rise to a simple graphical procedure for determining the total allowable catch (TAC). On a plot of yield versus effort, the most recent point (f_{n-1}, Y_{n-1}) is located and a straight line drawn through the origin. The intersection of this line and the vertical line through f_{MSY} locates the TAC point (Fig. 5).

The response indicated here is adequate when the reduction in biomass has not been too extreme, e.g. when P_{n-1}/P_∞ is still larger than 25%. However, in cases where it is greater, the major consideration should be the recovery of the stock rather than the maximization of the yield. Accordingly, we shall calculate the time needed for recovery of the stock to the MSY level when initially it is very low.

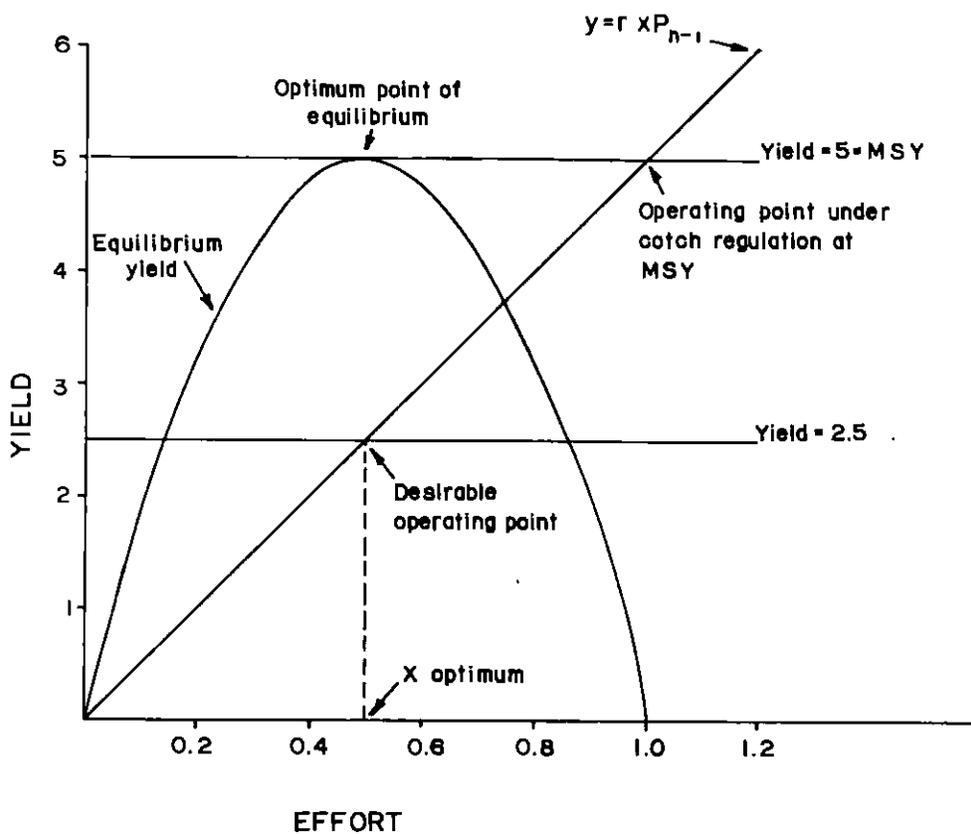


Fig. 4. Location of desirable operating points for an overexploited fishery. It is assumed the biomass has been reduced to $P_{\infty}/4$ in a fishery with $P_{\infty} = 100$ and $r = 0.2$.

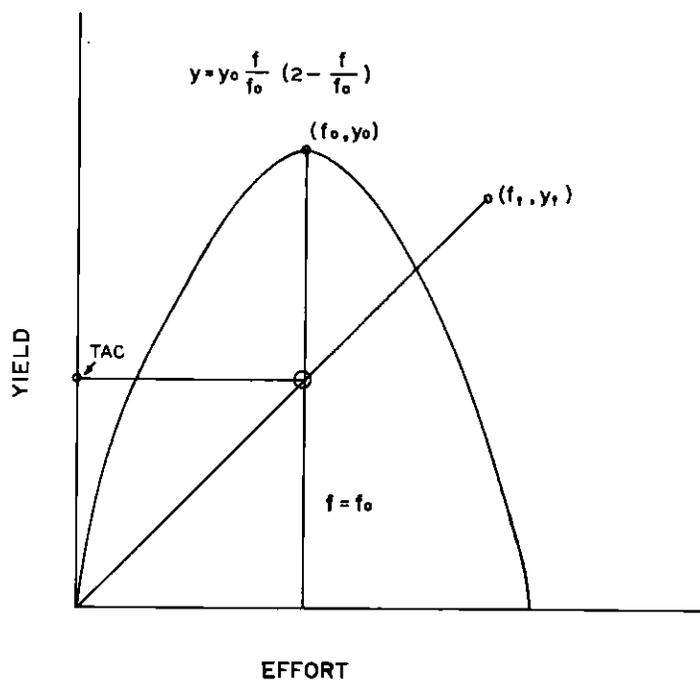


Fig. 5. Graphical method for determining TAC.

RECOVERY TIME OF OVEREXPLOITED STOCKS

Let us suppose the stock has been reduced to a level lower than $P_\infty/4$. Then the maximum speed of recovery is achieved when fishing effort is set at zero. We first calculate the minimum recovery time and then the appropriate levels of effort and yield to achieve recovery in a predetermined number of years.

The recovery time in the presence of fishing at the level x for n years is obtained by first solving equation (1) for P_n when the initial level is some P_0 less than $P_x/4$. The solution is:

$$P_n = \frac{P_\infty(1-x)}{1 - \left[1 - (1-x)\frac{P_\infty}{P_0} \right] \cdot \exp[-(1-x)rn]} \quad (32)$$

which is set equal to $P_\infty/2$, and after inverting both sides, becomes:

$$2(1-x) = 1 - \left[1 - (1-x)\frac{P_\infty}{P_0} \right] \cdot \exp[-(1-x)rn]. \quad (33)$$

This may be solved for n to obtain:

$$n_x = \frac{1}{(1-x)r} \cdot \ln \left[\frac{(1-x)\left(\frac{P_\infty}{P_0}\right) - 1}{(1-2x)} \right], \quad (34)$$

which will be minimized when $x = 0$ and will be infinite when $x = \frac{1}{2}$. Thus the fastest possible recovery when, say $P_0/P_\infty = 0.1$ would be:

$$n_0 = \frac{1}{r} \ln \left(\frac{P_\infty}{P_0} - 1 \right) = \frac{1}{r} \ln(q) = \frac{2.2}{r}. \quad (35)$$

This would be 11 years when $r = .2$, the value used in our example.

If a particular recovery time has been specified, equation (33) may be solved for the particular value of x that will bring it about. We shall obtain an upper bound for this value in terms of the maximum recovery time n_x . It may be obtained by taking the ratio of (34) to (35) which is:

$$\frac{n_x}{n_0} = \frac{1}{1-x} \cdot \frac{\ln \left[\frac{(1-x)\left(\frac{P_\infty}{P_0}\right) - 1}{(1-2x)} \right]}{\ln \left(\frac{P_\infty}{P_0} - 1 \right)}. \quad (36)$$

Since the quotient $[(1-x)(P_\infty/P_0)-1]/(1-2x)$ is an increasing function of x , it is larger than its value at $x = 0$. Hence we see that

$$\frac{n_x}{n_0} \geq \frac{1}{1-x} \cdot \frac{\ln \left(\frac{P_\infty}{P_0} - 1 \right)}{\ln \left(\frac{P_\infty}{P_0} - 1 \right)} = \frac{1}{1-x}$$

from which by solving for x we obtain:

$$x \leq 1 - \frac{n_0}{n_x}. \quad (37)$$

For example, if $r = 0.2$, and $P_0/P_\infty = 0.1$, and if we wish the stock to recover in 15 years, we set the fishing effort limitation at

$$x \leq 1 - \frac{11}{15} = 0.27.$$

This approximation is valid only when n_0/n_x is quite close to 1. For other values we may solve (36) for x numerically, or we may interpolate linearly between $x = 0$ and $x = \frac{1}{2}$. Then we obtain a slightly better estimate with the latter procedure. Indeed, since the function $(1-x)n_x/n_0$ is convex for x between 0 and $\frac{1}{2}$, it is greater than its linear interpolant, i.e.

$$(1-x) \frac{n_x}{n_o} \geq 1 - 4x \left(\frac{\frac{n}{4}(1-k)}{n_o} - 1 \right).$$

This may be solved for x to obtain the inequality:

$$x \leq \frac{\left(1 - \frac{n_o}{n_x} \right)}{1 + (4c-4) \frac{n_o}{n_x}} \quad (38)$$

where

$$c = \frac{(1-k)n}{4n_o} = \frac{\ln \left(\frac{3P_\infty}{2P_o} - 2 \right)}{\ln \left(\frac{P_\infty}{P_o} - 1 \right)}$$

For our previous example, with $n = 15$, we obtain the value:

$$x \leq 0.18$$

which is considerably smaller.

The corresponding values of yield may be obtained from equation (16) through substitution of the values of x obtained by equation (38).

APPENDIX

An example

The Atlantic mackerel fishery seems to fit the description of a fishery not in equilibrium and therefore amenable to our analysis. Anderson (MS 1975) has reviewed the status of this fishery for ICNAF Subarea 5 and Statistical Area 6. Using a modification of the method of Walter (1975), applied to his data, we are able to obtain an estimate for the MSY and the corresponding effort; these values are $MSY = 313,000$ tons and $f_{MSY} = 250,000$ standard US days. These estimates correspond to the equilibrium curve shown in Figure 6. On this same graph are plotted the yield and effort for the years 1968 to 1973.

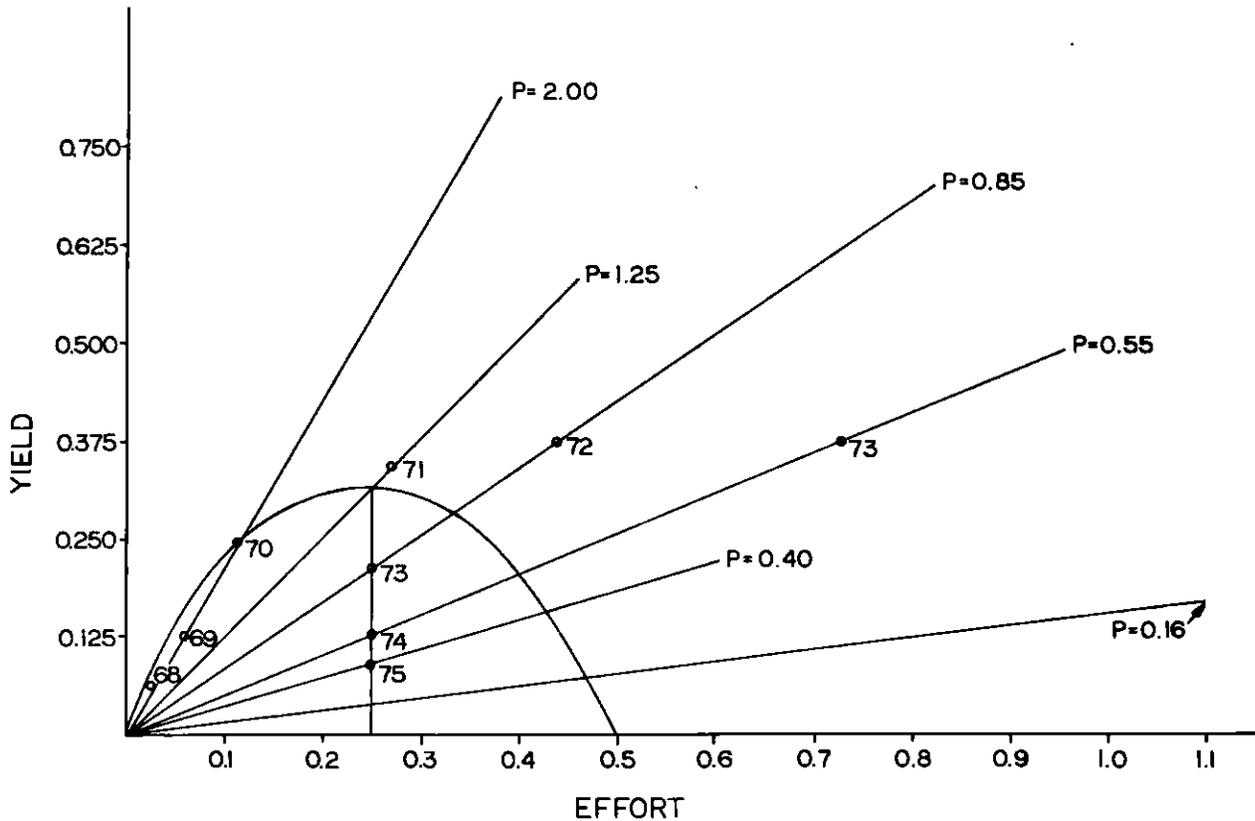


Fig. 6. Equilibrium yield curve for mackerel in ICNAF Areas 5 and 6. Straight lines radiating from origin are approximate annual yield curves for various values of biomass. Parameters were calculated to be $P_{\infty} = 2.5 \times 10^6$. Dots represent actual values and x's represent calculated TACs.

The value of r for this fishery was calculated indirectly by using the catchability coefficient q , which in turn was estimated from the fishing mortality $F = 0.6$ used in the mackerel assessment (ICNAF Redbook, 1974, p. 118) for 1973 and $F = 0.55$ used in 1972. The effort in those years was 719,000 and 461,000 days respectively. Since q^f and F both correspond to the same fishing mortality, the appropriate choice of q would be:

$$q = \frac{0.55 + 0.60}{0.719 + 0.461} \times 10^{-6} = 0.975 \times 10^{-6} \approx 1 \times 10^{-6}.$$

The equilibrium yield curve of equation (3) for this example would be:

$$y_e = 10^{-6} \cdot \frac{fP_{\infty}}{r} (r - 10^{-6} f).$$

With $f = f_{MSY}$, this must be equal to the MSY, i.e.:

$$(0.313 \times 10^6) = (10^{-6} \times 0.25 \times 10^6) \left(\frac{P_{\infty}}{r} \right) \left(r - (10^{-6} \times 0.25 \times 10^6) \right)$$

However, by equation (4) the MSY also equals $rP_{\infty}/4$. Hence we have:

$$rP_{\infty} = \frac{4(0.25P_{\infty})}{r}(r - 0.25)$$

which may be solved for r . The solution is:

$$r = 0.50,$$

the intrinsic growth rate for this stock of mackerel. The value of P_{∞} is now easily found. It is:

$$P_{\infty} = 0.313 \times 10^6 \times 4/r = 2.5 \times 10^6 \text{ tons.}$$

Using this value, the stock biomass for any year may be estimated by drawing a line through a point (f , y) corresponding to actual effort and catch and the origin. The intersection of this line and the vertical line through f_{MSY} will give the TAC and the stock biomass as a fraction of $P_{\infty}/2$. Thus, in Figure 6, it may be observed that the stock biomass in 1971 was at $P_{\infty}/2$ or 1.25×10^6 , in 1972 it was at $P = 0.85 \times 10^6$, and in 1973 at $P = 0.55 \times 10^6$. The total allowable catch for each year by this method should have been as follows:

Year	1971	1972	1973	1974
TAC	313	313	213	138.

In order to estimate the TAC for 1975 we must first calculate the stock biomass for 1974. This may be done by using equation (8), and hence

$$P_{74} = 0.40 \times 10^6.$$

Accordingly, the TAC for 1975 should be 100,000 tons, if recovery to the MSY level is desired. If the biomass is to be sustained at the 1974 level, a catch of up to 156,000 tons could be allowed. A catch in excess of this would cause the stock to decline further according to the model.

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Environmental Fluctuations and Fisheries Management¹

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ABSTRACT

The effect of random fluctuations in production on the success of fisheries management schemes is examined using a discrete version of Schaefer's (1954) model. Control of stock biomass, catch, and effort are considered. The average yield taken is shown to be inversely related to yearly fluctuations in yield. Control of stock biomass maximizes the average yield at the cost of large fluctuations in catch. Control of catch requires a large reduction in average yield to obtain stability. The effects of controlling effort lie between those of controlling biomass and controlling catch.

The restoring force of an exploited stock to deviations from equilibrium is examined and the presence of a critical zone of biomass less than one fourth of the virgin biomass in which further displacement weakens the restoring force and from which recovery of stock biomass is slow is noted. It is shown that control of effort at a level corresponding to an equilibrium biomass of two thirds the virgin stock instead of one half as is commonly recommended achieves a reduction in catch variance of from 60% to 75% and an increase of catch per unit effort of 33-1/3% with a loss in yield of 11%. The biomass buffer between equilibrium biomass and the critical zone is increased 133%, making the stock more resilient to depletion by a succession of weak year classes and reducing the need for rapid changes of regulations based on preliminary estimates of incoming year-class strength.

INTRODUCTION

"The preceding analysis assumes that the only variable factor affecting the fish stocks is the amount of fishing, but other, environmental, factors can have big effects. One of these is the variation in recruitment, ..." (Gulland, 1969). This caveat can be appended to almost any stock assessment. In this paper, the theoretical consequences of recruitment-induced fluctuations in production on fisheries management are examined and shown to be serious. The fisheries manager must balance stability and yield and cannot ignore one in search of the other.

MSY and Yield per Recruit

Various definitions of maximum sustainable yield (MSY) are possible. One possibility is to define the MSY of a stock as the maximum long-term average yield in weight which may be removed from a stock. Implicit in this definition is a range of management strategies, over which the yield is optimized, and the conservation of the stock (extinction implies a long-term average yield of zero). A more restrictive definition would require that the same yield be taken each year.

In the absence of recruitment fluctuations, there is no difference between these two yields, but, if fluctuations are present, the latter yield is considerably smaller than the former, as will be shown below, due to the inevitable drift of the spawning stock biomass into a zone of low recruitment.

Many stock assessments for the ICNAF area are based on the concept of maximizing the yield per recruit. Managing on this basis ensures a maximal catch for a given mesh selection curve from year-classes which have recruited, but ignores the conservation of the spawning stock. Sustainability of the maximum yield per recruit depends entirely on the wisdom of the scientists who determined mesh size regulations years ago and is not, in any sense, guaranteed.

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Stock and Recruitment

The problem of relating the state of a fish stock to its recruitment is the object of much recent research. The assumption that recruitment is independent of stock size for a wide range of stock sizes, which formed the basis of Beverton and Holt's (1957) manual is no longer considered tenable. Recent analysis of the North Sea plaice stock, for example, indicates a clear relationship between stock biomass and recruitment (Lett, personal communication). Two recent ICES symposia have dealt with this problem (Parrish [Ed], 1973; and ICES Symposium on changes in North Sea fish stocks and their causes, Aarhus, 1975).

The function of stock size used to predict recruitment has evolved from abundance indices (Beverton and Holt, 1957) to numbers of adults (Ricker, 1958) to biomass in conjunction with temperature (Lett *et al*, 1975). It appears that spawning stock biomass can be manipulated to maximize average recruitment although fluctuations due to environmental variables and species interactions remain.

It is easy to show that, if production (i.e., recruited biomass plus biomass gained by growth less biomass lost by natural mortality) is distributed about a mean which is a function of spawning stock biomass, then the long-term average yield is maximized by controlling the spawning stock biomass at the appropriate level. This has been demonstrated in papers by Ricker (1958) and Larkin and Ricker (1964) by simulating a model relating stock numbers to recruitment. Unfortunately, as Allen (1973) pointed out, this strategy transmits all variations in production to variations in catch which could cause economic chaos.

In this paper, attention is focused on a model derived from that of Schaefer (1954) by imposing discrete time units of one year. This modification facilitates analysis and is in better agreement with the yearly recruitments which comprise most of the production of stocks in the ICNAF area. It is assumed that the relation between biomass and production is quadratic. Although this model can profitably be refined to include the peculiarities of particular stocks, it is simple and robust and gives a good approximation, for example, to the stock and recruit relation of Gulf of St. Lawrence mackerel (Fig. 1).

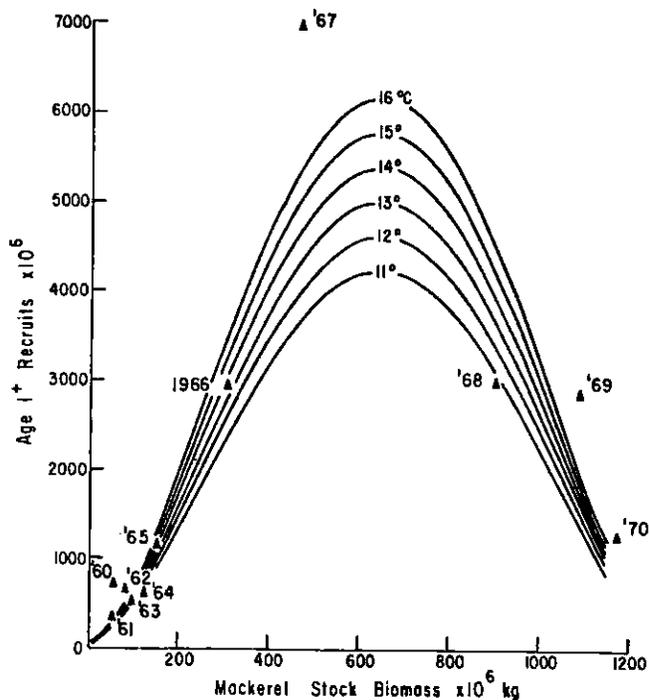


Fig. 1. Biomass and recruitment relation for mackerel in the Gulf of St. Lawrence (from Lett *et al.*, MS 1975).

For analytical convenience, a one-year lag time is employed and most of the analysis assumes a constant variance in production with statistically independent deviations from year to year. Unless successive deviations are negatively correlated, these assumptions tend to result in underestimates of the influence of fluctuations. The alternative of log-normal fluctuations was examined in some simulations with similar results.

THE MODEL

Notation

- B - stock biomass relative to virgin stock biomass $0 \leq B \leq 1$
B_{eq} - equilibrium stock biomass
P - yearly production
A - constant defining production/biomass (P/B) ratio at B = 1/2
F - effort scaled so that $0 \leq F \leq 1$ and F = 1/2 corresponds to equilibrium biomass B = 1/2
Y - yield
 ϵ - normally distributed random variable with mean 0 and variance σ^2
E - mathematical expectation

Derivation

In the notation of this paper, Schaefer's (1954) model has the form

$$\frac{dB}{dt} = AB(1-B) \quad (\text{Eq. 2 of Schaefer})$$

with a rate of catch per unit effort

$$\frac{d(\text{catch})}{Fdt} = k_2B \quad (\text{Eq. 5 of Schaefer})$$

or
$$\frac{d(\text{catch})}{dt} = FAB.$$

Setting $dt = 1$ to change to discrete form and adding the random variations (ϵ) in change of biomass, we have for the yearly production and the yield respectively

$$P = AB(1-B) + \epsilon \quad \text{and} \quad Y = FAB.$$

It is assumed that the ϵ 's for different years are statistically independent.

The restoring force at biomass B (i.e. the expected increment in B) towards the point $Y = E(P)$ is

$$E(P) - Y = AB(1-B-F)$$

which is zero at the deterministic equilibrium value $B_{eq} = 1-F$. The relation of $E(P)-Y$ to B together with the variance (σ^2) determines the magnitude of fluctuations in production and hence the size of the random displacements from equilibrium. The net change in biomass toward equilibrium in one year is $P-Y$.

The use of the virgin stock biomass ($B = 1$) as a reference point is analytically convenient. However, in practice, this biomass is poorly defined and poorly estimated, so that another reference point such as equating $B = 1/2$ with the biomass associated with the level of fishing mortality maximizing yield per recruit and average recruitment is better.

Constant Catch and Constant Effort

Fig. 2 illustrates the expected restoring force to displacement of biomass when a fishery is managed by constant catch and by constant effort when $A = 1$ corresponding to a P/B ratio of 1/2 when $B = 1/2$. Attempting to take the MSY catch each year results in extreme instability with a negative restoring force to displacement below $B = 1/2$. A small

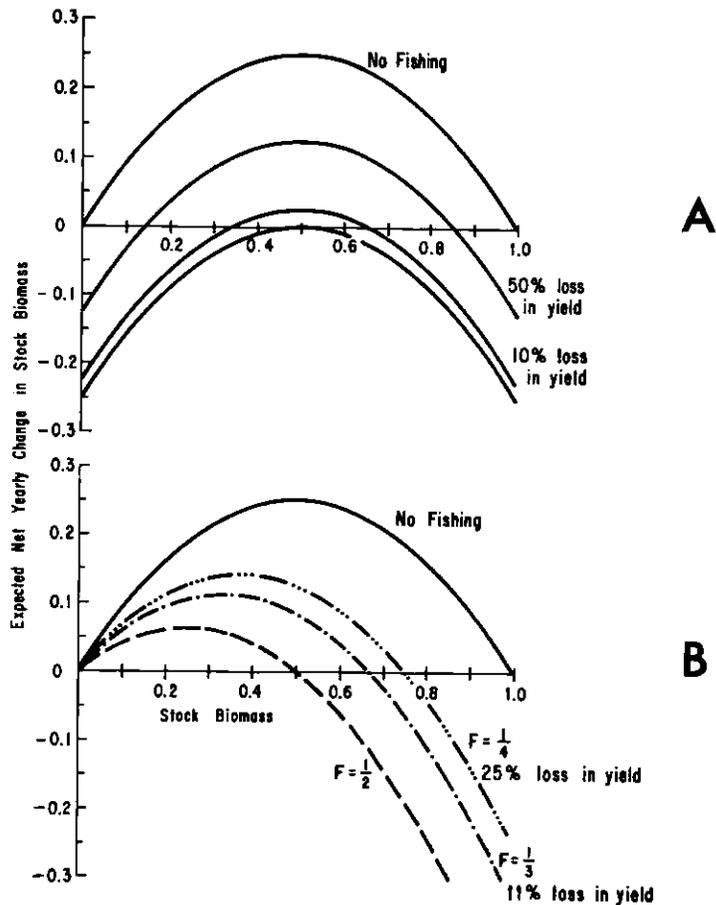


Fig. 2. A. Expected restoring force to displacements from equilibrium under a strategy of constant catch quotas. B. Expected restoring force to displacements from equilibrium under a strategy of constant fishing effort.

displacement would be followed by successively larger displacements until the stock biomass becomes zero. By comparison, management of effort at $F = 1/2$ which would give the same yield in the absence of fluctuations allows a positive restoring force to displacement below equilibrium. This is due to reduction in Y so that $P - Y$ is positive. The results of various attempts to increase stability at the cost of yield are also illustrated. A much greater loss in yield is required when holding catch fixed to produce the same maximum restoring force as when effort is fixed.

When the stock is exploited at $F = 1/2$, the restoring force increases with increasing deviations below $B = 1/2$ until the point $B = 1/4$ is reached. Further deviation of B below $1/4$ results in a decrease in the restoring force. Thus, the region, $0 < B < 1/4$, is a critical zone from which the ability of the stock to recover is impaired. If the biomass enters this zone, yield is reduced for several years and a complete collapse is risked.

Observe that setting $F = 1/3$ giving an equilibrium biomass of $2/3$ considerably increases the maximum restoring force and increases the biomass buffer separating equilibrium biomass from the critical zone by 133%. This strategy makes the stock much more robust in response to environmental fluctuations while losing only 11% of yield.

As F decreases from $1/2$ the average yield at B_{eq} decreases slowly at first and then more rapidly. If $F = 1/2 - \delta$, then

$$\begin{aligned}
 Y &= A(1/2 - \delta)(1/2 + \delta) \\
 &= A(1/4 - \delta^2).
 \end{aligned}$$

The effects of changes in F on variation of yield and on the biomass buffer also change continuously. The value of $F = 1/3$ was chosen for close examination because the loss in yield is modest while the benefits are considerable. In practice, a level of F could be chosen to correspond to the size of A and σ^2 so that an acceptable level of catch variation and of biomass buffer size is obtained.

If practically possible (the three-year lag time between collection of data and change in quotas by ICNAF is a serious difficulty), regulating the biomass at $B = 1/2$ produces the maximum sustainable yield. Slobodkin (1973) remarked that MSY seems to be obtained with biomass 40-60% of the virgin biomass for a wide range of models. If σ^2 is large, the resulting fluctuations in yield may be unacceptable. Thus, there is an incentive to examine how regulation of effort affects fluctuations in yield.

Linear Approximation

In the neighbourhood of B_{eq} , the restoring force for fixed effort may be approximated by the line

$$P - Y = (B_{eq} - B)AB_{eq}$$

with slope AB_{eq} . This approximation has an error term $A(B - B_{eq})^2$ proportional to the squared displacement of B from B_{eq} . The % error is

$$\frac{100(B_{eq} - B)}{B}$$

Thus, the restoring force is consistently overestimated and the variance of B and Y will be underestimated.

Using the linear approximation and writing $B(t)$ for the biomass at time t, if $E[B(t-1)] = B_{eq}$, then

$$E(P - Y) = (B_{eq} - B_{eq})AB_{eq} = 0,$$

so $E[B(t)] = B_{eq} = 1 - F$.

Thus, B_{eq} is a first order approximation to the mean biomass when the fishery is in statistical equilibrium.

Writing Σ^2 for the variance of B at statistical equilibrium, we have

$$B(t+1) = B(t) + [B_{eq} - B(t)]AB_{eq} + \epsilon$$

so that $\text{Var}[B(t+1)] = \text{Var}[B(t)][1 - AB_{eq}]^2 + \sigma^2$

and at equilibrium

$$\text{Var}[B(t+1)] = \text{Var}[B(t)] = \Sigma^2.$$

Therefore $\Sigma^2 = \frac{\sigma^2}{2AB_{eq} - (AB_{eq})^2}$.

Fig. 3 shows Σ^2/σ^2 as a function of AB_{eq} . As F approaches unity, AB_{eq} approaches zero and Σ^2 increases without limit. Reducing F reduces Σ^2/σ^2 until $AB_{eq} = 1$ when the variance ratio begins to increase.

The high variance ratios for AB_{eq} near zero are due to removing nearly all the standing stock each year. The high variance ratios for AB_{eq} near 2 are due to overcorrection for displacements so that biomass oscillates from side to side.

Simulations indicate that the approximation underestimates Σ^2/σ^2 by 10-20% for $A = 1$, $\sigma = 0.1$, with a higher % error for $\sigma = 0.05$, and is unreliable if $\sigma = 0.15$. The approximation does, however, show trends in the variance ratio correctly.

Increasing B_{eq} from $1/2$ to $2/3$ reduces Σ^2 if A is less than 1.6. To calculate the variance of Y, Σ^2 is multiplied by $(AF)^2$, and thus $\text{Var}(Y)$ is reduced by a factor of $1/4$ for $F = 1/2A$ and by a factor of $1/9$ for $F = 1/3A$. Thus, environmental fluctuations are

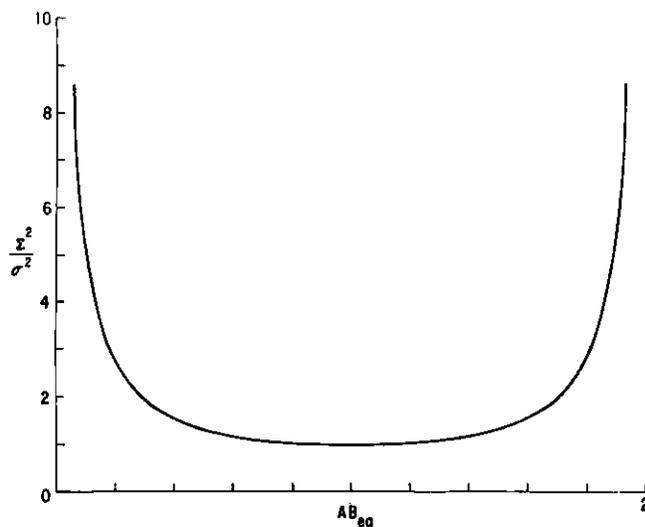


Fig. 3. Approximate relation of the variance ratio of stock biomass (Σ^2) to yearly production (σ^2) for a range of model parameters (see text).

partly absorbed by changes in biomass and partly by changes in yield. Increasing B_{eq} from 1/2 to 2/3 reduces the variance in yield by more than 50%, and an increase to 3/4 reduces the variance in yield by 75%. Simulations indicate a reduction in variance of yield by about 60% for the change of B_{eq} from 1/2 to 2/3.

Shift of Equilibrium

Because the slope of the restoring force decreases for negative deviations and increases for positive ones, σ^2 affects the equilibrium biomass for a given effort F . Thus

$$E[B(t+1)] = E[B(t)] + E[AB(1-B-F)]$$

so that at equilibrium

$$E[AB(1-B-F)] = 0$$

Let this equilibrium biomass be B^* . Then

$$E[AB] - E[AB^2] - E[ABF] = 0$$

$$(B^*)^2 - (B^*)B_{eq} + \Sigma^2 = 0$$

or
$$B^*(B_{eq} - B^*) = \Sigma^2 \quad (\text{so that } B^* < B_{eq})$$

and
$$\frac{B_{eq} - B^*}{B_{eq}} = \frac{\Sigma^2}{B^*B_{eq}}$$

Thus, the relative loss in equilibrium biomass due to fluctuations in biomass for a fixed level of effort is approximately the squared coefficient of variation of biomass. Because of this, the average yield for a given effort F is less than AB_{eq} and the loss is smaller for larger values of B_{eq} . The loss in yield from this factor is less than 10% and, in most cases, less than 5%.

Simulations

Simulations were carried out to examine the effect of reduction of F from 1/2 to 1/3 and 1/4 for various values of A and σ^2 . The results are shown in Table 1. Examples of 50-year simulations are shown in Fig. 4 and 5.

In the simulations, variance in catch was reduced 60% by setting $F = 1/3$ and almost 80% by $F = 1/4$. The loss in average yield was about 11% for $F = 1/3$ and 25% for $F = 1/4$. The loss in yield with $F = 1/3$ consisted of missed large catches while small catches were not affected. Thus, the practical consequences of the reduced average yield are minimized and are more than compensated for by the 33% increase in average catch per unit effort. In some simulations with $F = 1/2$, the stock biomass entered the critical zone and for several consecutive years produced lower yields than the same stock with the same environmental fluctuations regulated at $F = 1/3$.

Some simulations were carried out with $\ln(\epsilon)$ normally distributed with mean 0 and variance σ^2 . In these, the reduction of F from $1/2$ to $1/3$ resulted in a 14% loss of yield and a 70% reduction in variance.

Table 1. Simulation results at different values of A , σ and F for $\epsilon \sim N(0, \sigma^2)$ in the upper part, and $\ln(\epsilon) \sim N(0, \sigma^2)$ in the lower part of the table.

A	σ	F	Years	Mean Yield	%	Variance	%
1.0	0.1	1/2	1000	0.244	100	0.00374	100
1.0	0.1	1/3	1000	0.221	90.6	0.00153	40.9
1.0	0.1	1/4	1000	0.187	76.6	0.00081	21.7
1.0	0.05	1/2	1000	0.252	100	0.001020	100
1.0	0.05	1/3	1000	0.223	88.5	0.000379	37.2
1.0	0.05	1/4	1000	0.188	74.6	0.000200	19.6
1.0	0.2	1/2	61	Extinct			
1.0	0.2	1/3	461	Extinct			
1.0	0.2	1/4	464	Extinct			
1.5	0.1	1/2	100	0.370	100	0.00846	100
1.5	0.1	1/3	100	0.332	89.7	0.00329	38.9
1.5	0.1	1/4	100	0.280	75.7	0.00181	21.4
1.5	0.15	1/2	100	0.338	100	0.0227	100
1.5	0.15	1/3	100	0.323	95.6	0.00769	33.9
1.5	0.05	1/2	100	0.378	100	0.00207	100
1.5	0.09	1/3	100	0.335	88.6	0.000806	38.9
1.5	0.05	1/4	100	0.282	74.6	0.000442	21.4
0.5	0.1	1/2	100	0.122	100	0.00259	100
0.5	0.1	1/3	100	0.113	92.6	0.000766	29.6
0.5	0.1	1/4	100	0.0955	78.3	0.00387	14.9
0.5	0.15	1/2		Extinct			
0.5	0.15	1/3	100	0.105		0.00205	

1.0	0.1	1/2	100	0.255	100	0.000326	100
1.0	0.1	1/3	100	0.224	87.0	0.000090	27.6
1.0	0.4	1/2	100	0.268	100	0.004832	100
1.0	0.4	1/3	100	0.231	86.2	0.00144	29.8
0.5	0.4	1/2	100	0.140	100	0.000619	100
0.5	0.4	1/3	100	0.118	84.3	0.000158	25.5

Sources of Error

There are many possible sources of bias and sampling error in estimating biomass and yield. In view of the asymmetry of the restoring force of a stock to displacement above and below B_{eq} and the lag time of years involved in recognizing and correcting errors in estimates, it is wise to err on the size of setting B_{eq} too high rather than too low.

Fitting a Schaefer model by a regression of catch per unit effort on effort in a declining fishery is likely to overestimate the MSY, although it should produce better estimates of the appropriate effort level.

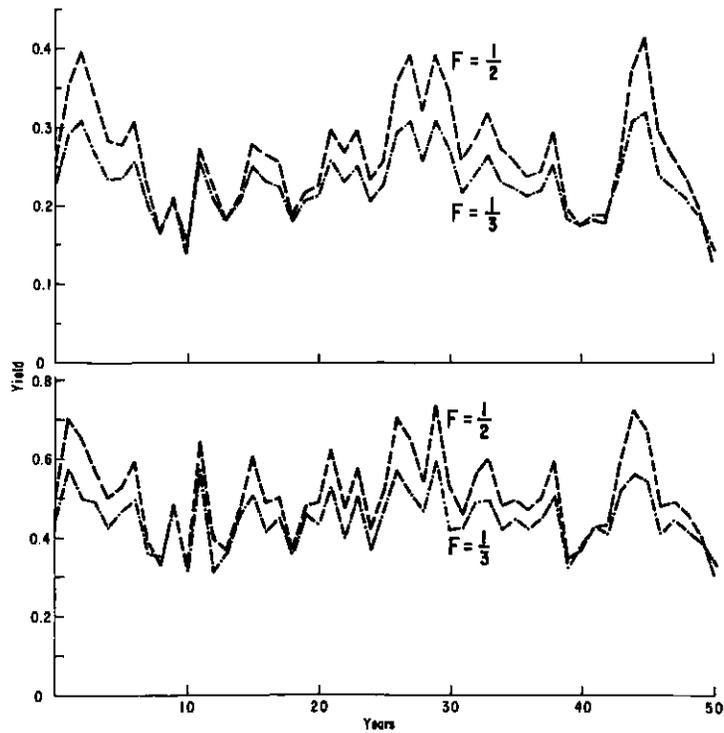


Fig. 4. Simulated catches for normally distributed ϵ with $\sigma = 0.1$ and $A = 1$ (above), and for normally distributed ϵ with $\sigma = 0.1$ and $A = 2$ (below).

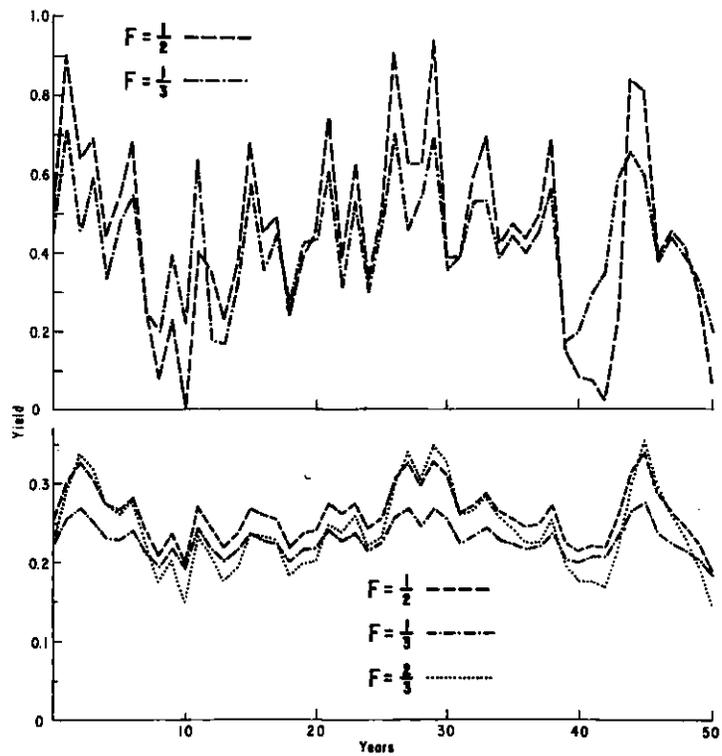


Fig. 5. Simulated catches with normally distributed ϵ with $\sigma = 0.2$ and $A = 2$ (above), and with log normally distributed ϵ with $\sigma = 0.1$ and $A = 1$ (below).

Multi-species Fisheries

When catching groundfish with an otter trawl, it is impossible to direct fishing effort accurately at one species. Even if the production *versus* biomass and effort *versus* yield relationships for a number of species were such that the same level of effort resulted in the MSY for all, there is a serious danger in treating the fluctuations in combined yields as if they were from a single stock.

The difficulty is that, with a high level of exploitation, individual stocks are likely to fluctuate into the critical zone of less than 1/4 of the virgin stock biomass from which they recover slowly. These stocks would be held down, as is the case with North Atlantic haddock stocks, by the removals as by-catch in fisheries aimed at other groundfish. Thus, the spectre of stock after stock fluctuating into the critical zone with a steady decrease in overall arises. In the presence of multi-species fisheries, it is essential to maintain a sufficient buffer of biomass for each component stock to ensure that it stays in the region where restoring force increases with displacement from equilibrium.

CONCLUSIONS

In the presence of fluctuations in production, attempting to remove the MSY yield each year from a stock leads to disaster. Management of the stock biomass within narrow limits enables the MSY to be taken on the average but passes on environmental fluctuations to the catch. Management of a stock by fixing effort allows some of the fluctuations to be absorbed by the stock and some by changes in yield.

An excellent compromise between yield, stability, and conservation is to fix fishing effort at a level corresponding to an equilibrium biomass at 2/3 the virgin stock biomass. The loss in yield is 11%, with a reduction in variance of yield of 60-70%, an increase in catch per unit effort of 33% and an increase of the biomass buffer between equilibrium and the critical zone of 1/4 or less of the virgin biomass of 133%.

In the context of the groundfish fishery on the Scotian Shelf, following the analysis of Halliday and Doubleday (1975), a 60% reduction in fishing effort is required to achieve an equilibrium biomass of 2/3 the virgin biomass. This could be carried out in phased reductions.

It must be emphasized that the above analysis is theoretical, applying only when Schaefer's (1954) model is applicable. Similar results will apply, for example, to generalized production models with a one-year lag between spawning and recruitment. If a lag of more than one year exists between spawning and recruitment, a cyclic tendency results. Examination of these generalizations is outside the scope of this paper.

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Interactive Fisheries: A Two Species Schaefer Model

by

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ABSTRACT

A two species fishing model is considered and compared with the results from a grouped Schaefer model. If fishing effort is proportional to the relative number of each species, then it is shown that the correspondence between the two models diverges as the ratio of the two species diverges from unity. It is also shown that fishing each species in proportion to their relative numbers does not necessarily take the fishery through its maximum sustainable yield.

INTRODUCTION

Schaefer (1954, 1957) developed a model to evaluate the equilibrium yields from a fishery. This model assumes that the rate of change of stock biomass can be represented as:

$$\frac{dS}{dt} = AS - BS^2 - qFS$$

where S is the stock biomass, A and B are parameters of the stock population growth, and q and F are the familiar parameters of catchability and fishing mortality. Gulland (1974) has pointed out that the Schaefer model is identical with the assumption that catch per unit of effort is linearly related to effort. Among others, Pinhorn (1976) and Brander (1975) have fitted Schaefer models to total fish biomass in an area and here the parameters A and B take on different meanings, A being the net rate of increase at low total biomass levels and B representing the interspecific and intraspecific density dependent regulation. This study, through consideration of a two species model, helps to elucidate the relationship between these two applications of the Schaefer model.

THE MODEL

Let us assume a fishery on two stocks where the fishing effort on the individual stocks is proportional to the relative numbers of fish in each stock. To avoid proliferation of the parameters, the catchability is put at 1.0 and the preferability of the two species to the fishermen is considered to be the same. This situation may then be expressed as

$$\frac{1}{p} \frac{dp}{dt} = a_1 - b_1 p - F \left(\frac{p}{p+r} \right) \quad (1)$$

$$\frac{1}{r} \frac{dr}{dt} = a_2 - b_2 r - F \left(\frac{r}{p+r} \right) \quad (2)$$

where p and r are the respective biomasses of the two stocks. In the equilibrium state (r^* , p^*), $dp/dt = dr/dt = 0$, and hence

$$r^* = \frac{a_2 p^*}{(a_1 - p^*(b_1 - b_2))} \quad (3)$$

and p^* is given by solving the quadratic

¹ Submitted to the Seventh Special Commission Meeting, September 1975 as Res.Doc. 75/IX/125.

$$p^2 b_1 (b_1 - b_2) + p[F(b_1 - b_2) - a_1(b_1 - b_2) - a_1 b_1 - a_2 b_1] + (a_1 a_2 + a_1^2 - a_1 F) = 0 \quad (4)$$

The equilibrium yield is given by (dropping asterisks)

$$\frac{F(p^2 + r^2)}{p + r} \quad (5)$$

As will be appreciated from the form of Equation (4), general solutions for r^* and p^* are unwieldy, but in all the numerical examples given only one positive pair of r^* and p^* values exist; that is, for any value of F two positive equilibria do not exist.

General stability criteria for the equilibria cannot be evaluated owing to the large number of parameters, but the stability of any specific case can easily be dealt with, and, in general, it must be noted that these are a very stable set of equations and unstable equilibria would not be expected. The investigative techniques may be obtained from May (1973) and Beddington (1974).

If Equations (1) and (2) are added together, the relationship between the two sorts of Schaefer models can be seen:

$$\frac{dr}{dt} + \frac{dp}{dt} = a_1 p + a_2 r - b_1 p^2 - b_2 r^2 - \frac{F(p^2 + r^2)}{p + r}$$

If $p + r = S$, then

$$\frac{dS}{dt} = a_1 p + a_2 r - b_1 p^2 - b_2 r^2 - \frac{F(p^2 + r^2)}{S}$$

and if $p = r = S/2$, then

$$\frac{dS}{dt} = \frac{S(a_1 + a_2)}{2} - \frac{S^2(b_1 + b_2)}{4} - \frac{FS}{2}$$

which is identical with the Schaefer model for total stock biomass. However, as the ratio $p^*:r^*$ diverges from unity the two models diverge.

The simplest way of comparing the two models is to look at the yield per unit of effort against effort curve. By definition, the Schaefer model assumes a linear relationship and the degree of departure from linearity represents the departure from the Schaefer model.

If we arbitrarily select $a_1 = 0.35$ and $a_2 = 0.45$, then values of b_1 and b_2 can be obtained if we set $F = 0.2$ and vary the ratio of $p:r$ but keep $p + r = 2,000$. This gives

- a) If $p:r = 1:1$, then $b_1 = 2.5 \cdot 10^{-4}$ and $b_2 = 3.5 \cdot 10^{-4}$
- b) If $p:r = 1:3$, then $b_1 = 6.0 \cdot 10^{-4}$ and $b_2 = 2.0 \cdot 10^{-4}$
- c) If $p:r = 1:19$, then $b_1 = 3.4 \cdot 10^{-3}$ and $b_2 = 1.367 \cdot 10^{-4}$.

Hence, we have three arbitrary sets of values which, at $F = 0.2$, have the ratios of $p:r$ as given above. Equilibria values for p^* and r^* may be obtained from Equations (3) and (4) for different values of F , and hence the equilibrium yield from Equation (5). These are shown in Fig. 1. It will be noted that the characteristic parabolic yield curve is lost as the ratio of $p:r$ diverges from unity. This can be more easily seen in the graph of equilibrium catch per unit of effort against effort (Fig. 2) as the departure from linearity.

DISCUSSION

First, it may be asked if the incorporation of fishing effort in this way is valid. Obviously catchability and economic weighting of one species relative to another will complicate the real fishing strategy, but this could only increase the non-linear nature of the results, and probably the expression of fishing in this model is good for a fishery where total effort is fairly constant.

Second, it is noticeable that there is no real difference between the Schaefer model of total fish biomass and the sum of individual Schaefer models where the two species are in about the same proportions. However, as the ratio diverges from unity the two give

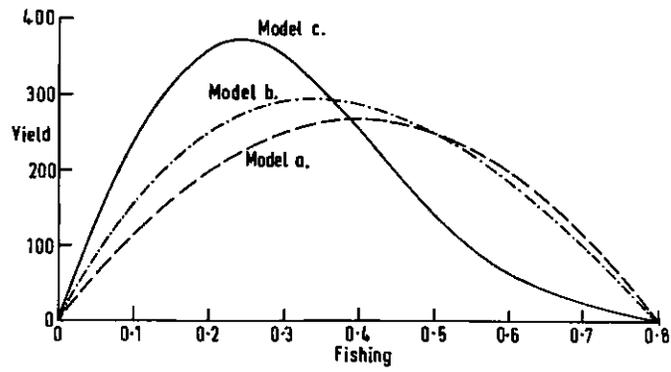


Fig. 1. Equilibrium yield and effort for the three sets of model values given in the text.

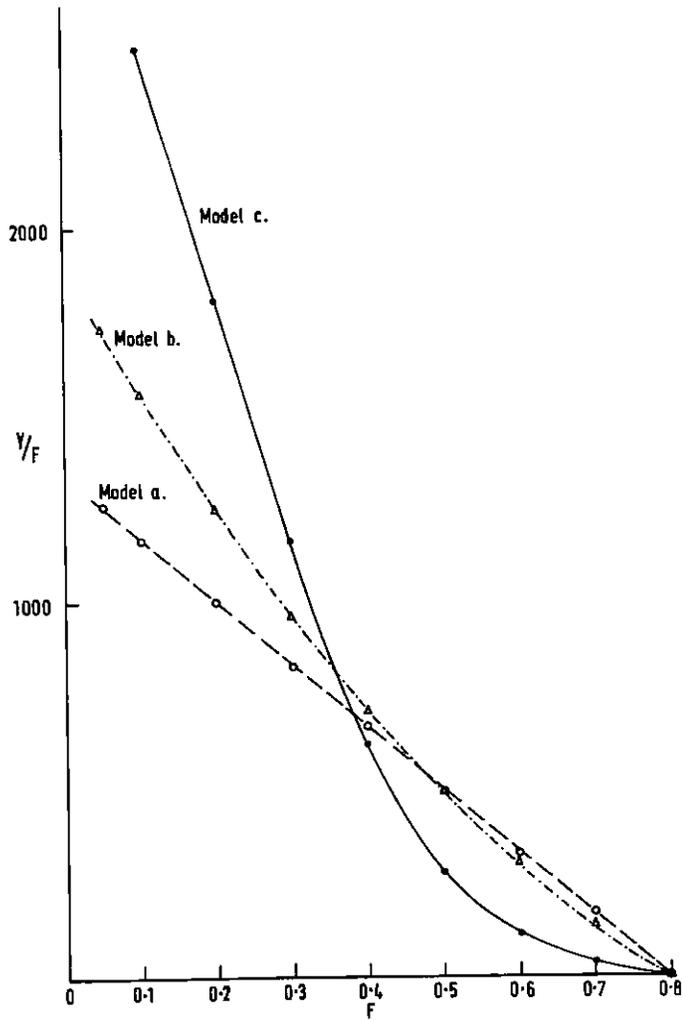


Fig. 2. Equilibrium Y/F against F for the three sets of model values given in the text.

quite different results. To fit a yield parabola through the origin one needs two or more points. If these are taken at $F = 0.1$ and 0.2 for $p:r = 1:19$ in Fig. 1, the resulting parabola reaches zero at about $F = 0.5$. This can be appreciated better from Fig. 2, where a straight line fitted through the corresponding two points gives an intercept at $F = 0.475$. Similarly, if the values at $F = 0.6$ and 0.8 are taken in Fig. 1, a long low parabola results, thus predicting a very low maximum sustainable yield.

The maximum sustainable yields for the type of fishing described here can be obtained from Fig. 2, but this is not necessarily the maximum sustainable yield that could be achieved if fishing were distributed differently. If the equilibrium populations of the two species are given by

$$a_1 - b_1 p^* - f_1 = 0$$

and

$$a_2 - b_2 r^* - f_2 = 0,$$

then the equilibrium yield is given by

$$\frac{f_1(a_1 - f_1)}{b_1} + \frac{f_2(a_2 - f_2)}{b_2}$$

and the resulting yield isopleths are given in Fig. 3, along with the locus of equilibrium yields for the original proportionate fishing model. It will be noted that, in this instance, the locus does not go through the maximum sustainable yield.

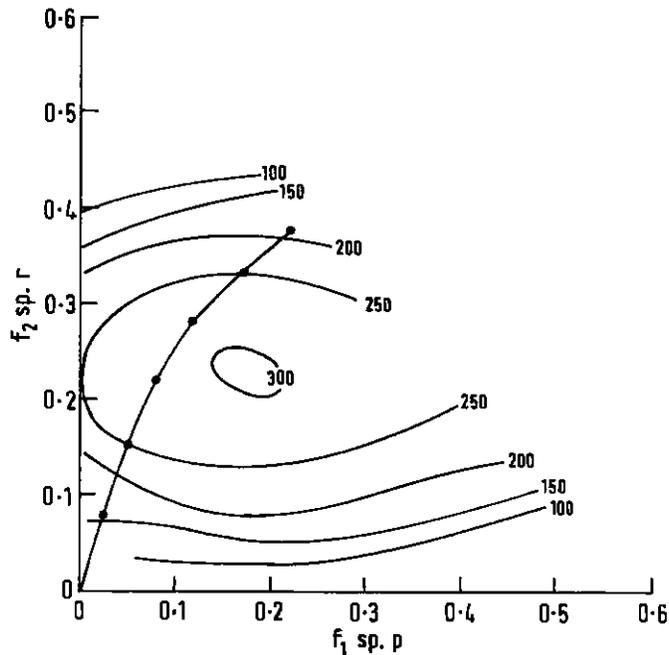


Fig. 3. Sustainable yield isopleths with the locus of yields obtainable with proportionate fishing.

In conclusion, two points are worth stressing. First, the two methods, (i) grouping fish species, and (ii) taking them as separate species related only by fishing, do not lead to the same results if the species are in differing proportions. This is not to say that one method is better than the other, for the underlying assumptions of the Schaefer model are nebulous. Second, in this simple although rational model, proportionate fishing does not necessarily take the fishery through the maximum sustainable yield.

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The Effect of Biological Interaction on the Theory of Mixed Fisheries

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INTRODUCTION

In order to examine in detail any fishery situation, it is necessary to postulate a model of how the fishery behaves. Single species management has been attempted by a variety of models. The most important of these to ICNAF assessments have been the dynamic pool model and the Schaefer model. For the study of mixed fishery problems, however, the Schaefer model has the great advantage of simplicity, and, consequently, the development of ideas on mixed fisheries in this paper follows that approach. Pope (MS 1975) has shown that a mixed fishery for two stocks can be represented in two dimensions as contours of equal total yield plotted against the fishing mortality for each species. If the two stocks have yield curves of a parabolic Schaefer form, the resulting contours of equal yield have the form of ellipses when plotted against the fishing mortality on each species. Furthermore, by-catch rates for the second species as a result of a directed fishery for the first species can be taken into account and *vice versa*. The maximization of physical yield then becomes an exercise in quadratic programming.

This approach indicated that, if a multiple species fishery conformed to this model and if the development of fishing effort on the system occurred as some constant ratio between species, the form of the yield curve for total catch would be a parabolic function of total effort. Pope (MS 1975) pointed out, however, that, unless the ratio of effort on species 1 to that on species 2 passed through the maximum attainable yield, the resulting yield curve obtained would neither indicate the true MSY catch from the system or the level of effort at which maximum yield would be attained. Another fact to emerge from this approach was that a total effort quota designed to obtain the MSY when applied in the right proportion could destroy one of the stocks if it were wrongly applied. This approach was unable to comment on the validity or otherwise of total yield curves based on fishing effort that had not developed on two species in a constant ratio. It was felt that most real fisheries would have developed in a less well-defined manner and that, therefore, the resulting yield curves based on total effort *versus* total catch per effort (for example, those developed by Pinhorn (1976) and by Halliday and Doubleday (1976)), might not necessarily indicate the true maximum yield from the various stocks. This mixed fisheries theory was open to criticism in that it did not take account of possible interactions between species and because it only indicated the stationary (equilibrium) behaviour of the system. In order to meet the first of these criticisms, this paper attempts to consider the effect of biological interactions between stocks.

BIOLOGICAL INTERACTIONS BETWEEN SPECIES

Walter (MS 1975) gives the non-steady state condition form of the Schaefer model as

$$\frac{1}{p} \frac{dp}{dt} = b - ap - qf \quad (1)$$

where p is population biomass of the stock, t is time, f is fishing effort, q is the catchability coefficient and b and a are parameters which characterize the stock. This can be extended in an obvious fashion to consider the effect of the interactions of a second population with biomass r . This results in the two equations

$$\frac{1}{p} \frac{dp}{dt} = b - ap \pm cr - qf \quad (2)$$

¹ Submitted to the Seventh Special Commission Meeting, September 1975 as Res.Doc. 75/IX/127.

$$\frac{1}{r} \frac{dr}{dt} = \hat{b} - \hat{a}r \pm \hat{c}p - \hat{q}\hat{f} \quad (3)$$

where the plain constants (a, c) indicate the parameters and fishing effort of stock 'p' and the hatted parameters (\hat{a} , \hat{c}) those of stock 'r'. When the two stocks are in equilibrium,

$$\frac{dp}{dt} = \frac{dr}{dt} = 0$$

and it follows that

$$b - ap \pm cr - qf = 0 \quad (4)$$

$$\hat{b} - \hat{a}r \pm \hat{c}p - \hat{q}\hat{f} = 0 \quad (5)$$

where the sign of c and \hat{c} are either both negative in the case of a competition model or negative and positive respectively in the case of a prey-predator model. The South African pilchard and anchovy fisheries reported on by Pope and Harris (MS 1975) form a possible example of the competition type of model. The interactions of, for example, the Newfoundland cod and capelin of Div. 2J+3KL would possibly furnish an example of the prey-predator model.

Some general conclusion can be drawn from the form of Equations (4) and (5). Assuming the sign of c and \hat{c} to be negative and by multiplying (4) by p and (5) by r, we obtain

$$bp - ap^2 - crp = \text{yield (p)} \quad (6)$$

$$\hat{b}r - \hat{a}r^2 - \hat{c}rp = \text{yield (r)}. \quad (7)$$

Therefore, if $Y = \text{yield (p)} + \text{yield (r)}$ (that is, the total yield), then

$$Y = -ap^2 - \hat{a}r^2 - (c + \hat{c})rp + bp + \hat{b}r. \quad (8)$$

Thus, within the area of validity of the model the yield curves would take the form of ellipses with their major axis inclined to the axis of population sizes. Also it follows from Equations (4) and (5) that

$$p = \frac{\hat{a}(b-qf) - c(\hat{b}-\hat{q}\hat{f})}{\hat{a}a - c\hat{c}} \quad (9)$$

$$r = \frac{a(\hat{b}-\hat{q}\hat{f}) - \hat{c}(b-qf)}{\hat{a}a - c\hat{c}} \quad (10)$$

and total yield

$$Y = Af^2 + \hat{A}\hat{f}^2 + (C+\hat{C})f\hat{f} + Bf + \hat{B}\hat{f} \quad (11)$$

where A, \hat{A} , C, \hat{C} , B and \hat{B} are functions of a, \hat{a} , b, \hat{b} , c, \hat{c} respectively.

The total yield from such a system also has contours of constant equilibrium yield in the form of ellipses, but these do not now have their major axis parallel to the axis of the fishing effort on the two species. The above argument thus leads to a solution similar to that described for the non-interactive fisheries, except that (i) the ellipses are now inclined to the coordinate axis of the system, and (ii) there are additional constraints on the system corresponding to the values of r and f at which p becomes zero and the values of p and f at which r becomes zero. From Equations (4) and (5) these are respectively

$$b - cr - qf \geq 0 \quad (12)$$

and

$$\hat{b} - \hat{c}p - \hat{q}\hat{f} \geq 0. \quad (13)$$

From Equations (9) and (10), these may be rewritten as

$$\hat{a}a(b-qf) - ca(\hat{b}-\hat{q}\hat{f}) \geq 0 \quad (14)$$

and

$$\hat{a}a (\hat{b}-\hat{q}\hat{f}) - \hat{c}\hat{a} (b-qf) \geq 0. \quad (15)$$

EXAMPLES OF INTERACTIVE MIXED FISHERIES

The consequences of the equations in the previous section are best seen in practical examples.

Pope and Harris (MS 1975) give an example of such an interactive fishery for the South African pilchard and anchovy. Figure 1 shows the form of the yield curves estimated for the total yield of these two stocks.

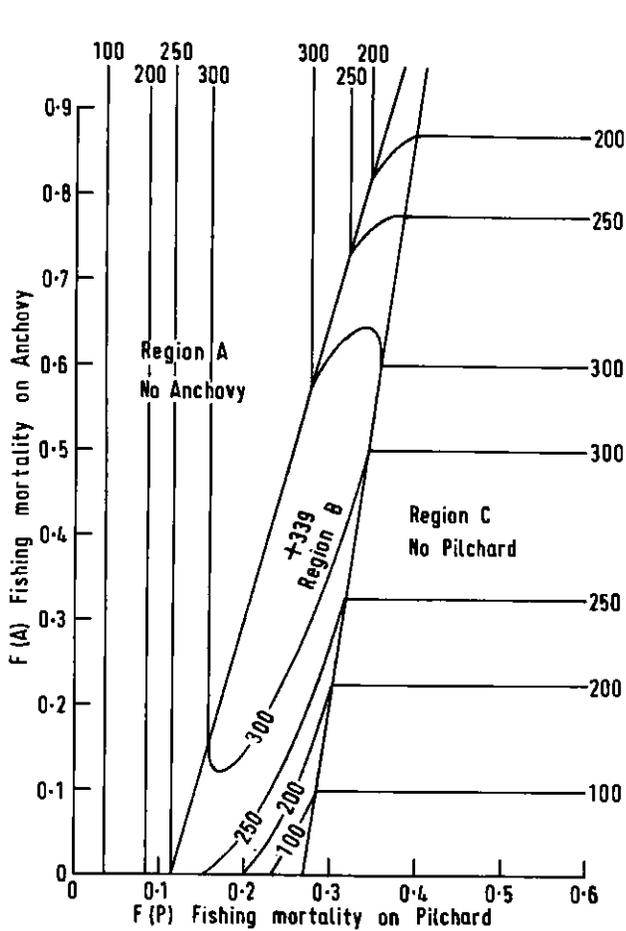


Fig. 1. Contours of total yield drawn against the fishing mortality of South African anchovy and pilchard and the region of mixed fishery (Region B) and of pure fisheries for the two stocks (Regions A and C).

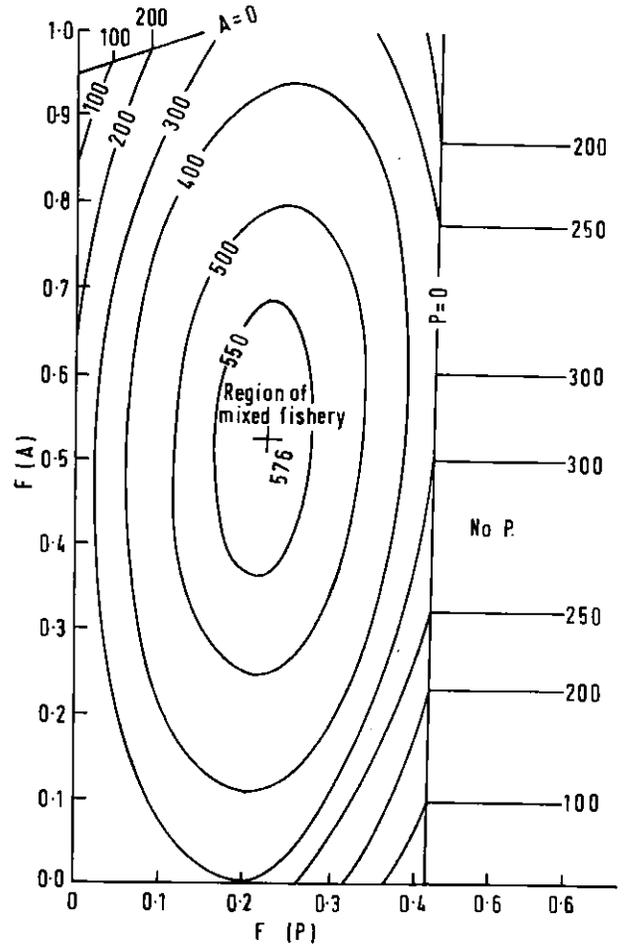


Fig. 2. As Fig. 1 but with the interaction terms reduced arbitrarily by an order of magnitude.

The equilibrium equations governing these yield functions are:

$$0.43 - 0.000143 P - 0.000143 A - F(P) = 0 \quad (16)$$

and

$$1.10 - 0.0001 A - 0.0005 P - F(A) = 0 \quad (17)$$

where P is the biomass of pilchard, A is the biomass of anchovy, and F(P) and F(A) are their respective fishing mortalities. The main features of the system are fairly apparent. The plot of total yield (Fig. 1) on the fishing mortality of the two species shows that the system has three modes of behaviour. In the first (Region A) the yield is composed

entirely of pilchard, and the anchovy biomass is zero. In Region B a mixed fishery for both species exists, and in Region C the pilchard biomass is zero with the yield composed entirely of anchovy. The boundaries between these regions are the constraints mentioned in the previous section. It is noticeable that the region of mixed fishery is a fairly narrow wedge, and that it would probably be difficult to control a fishery sufficiently closely to be sure that it will always lie inside this region. It is also noticeable that for this apparently highly interactive fishery the maximum yield attainable in the mixed fishery (340,000 tons) is only slightly larger than that which would be obtained in either of the pure fisheries (320,000 tons for pilchard and 302,000 tons for anchovy). Thus the effect of stock interactions is to reduce the total MSY of the system to below the sum of the individual species MSYs. The degree to which this occurs is a function of the degree of interaction between the stocks. This can be seen from the following modifications of Equations (16) and (17) made in order to change the interaction terms. In all of the following illustrative examples the only changes made to Equation (16) are to the coefficient of the A term and the only changes made to Equation (17) are to the coefficient of the P term. Consequently, outside the mixed fishery region B the yield of the single stocks in all examples are unchanged. The region of the mixed fishery will, however, be modified. The first example reduced the interactions by an order of magnitude. Thus, Equations (16) and (17) become

$$0.43 - 0.000143 P - 0.0000143 A - F(P) = 0 \quad (18)$$

$$1.10 - 0.001 A - 0.00005 P - F(A) = 0. \quad (19)$$

Figure 2 shows the resulting constraints and yield functions. It is apparent that the system is very similar to a non-interactive fishery (c.f. Pope, 1976) with the area of the mixed fishery considerably extended and the contours of total yield being concentric ellipses with axis almost parallel to the coordinates. The maximum yield (576,000 tons) is far closer to the sum of the two individual pure fisheries than was the case in Fig. 1. Figure 3 shows a situation halfway between Fig. 2 and 1. The equations governing this are

$$0.43 - 0.000143 P - 0.000118 A - F(A) = 0 \quad (20)$$

$$1.10 - 0.001 A - 0.000266 P - F(A) = 0. \quad (21)$$

In this case the total yield has a value of 415,000 tons and the region of mixed fishery is of intermediate size. It is interesting to contrast this with Fig. 4 which shows the yield when Equation (20) is modified to

$$0.43 - 0.000143 P + 0.000118 A - F(A) = 0 \quad (22)$$

and Equation (21) held the same.

The system thus described is a prey-predator model with the pilchard hypothetically preying on the anchovy. The general shape and size of the yield function in this case corresponds more nearly with the contours of Fig. 2 than Fig. 3, with the ellipses less inclined to the coordinate axis and rather fatter. The total yield in this case is 523,000 tons which is also closer to that in the less interactive case.

The examples thus show some of the effects of the interaction terms on the behaviour of the system. The chief features to note are that (a) for highly interactive fisheries the mixed fishery region is narrow, and (b) the phenomenon of the total biomass switching over from being mostly one species to mostly the other is likely to be observed if fishing is sufficiently intensive. Where interaction terms are lower or where they are of opposite sign (as in a prey-predator system), this is less likely to happen. When fisheries are highly interactive, it is also possible that the total yield is very little greater than that which would be achieved by the fishery for either component, if the other component became extinct. When they are not highly interactive, the total yield approximates to the sum of the yields of the individual species. In the connection it is pertinent to point out that, in practice, these individual yields would probably be assessed in the presence of the other species and not when it was extinct.

IMPLICATIONS OF THE THEORY TO THE MANAGEMENT OF MIXED FISHERIES

The effects of by-catch rates on the potential yield of the systems described by the models are the same as those described in Pope (MS 1975), that is to say, whether the true maximum yield of the stock is attainable or not will depend on whether the levels of fishing mortality giving the maximum yield lie within or without the sector defined by

the lines indicating the fishing mortalities which would be generated in the various directed fisheries. If this sector was narrow, i.e. the various fisheries had considerable overlap and by-catch rates were high, the total effort imposed on the system would generate mortalities in the two stocks which were in a fairly constant proportion. In these circumstances a total effort quota could be expected to be quite effective because the model, whether interactive or non-interactive, would have a parabolic yield function in the mixed fisheries region with respect to the total effort generated. In effect, the high by-catch rates would supply the individual stock management constraints. In these circumstances, however, it is improbable that the maximum attainable yield would be as high as the maximum sustainable yield.

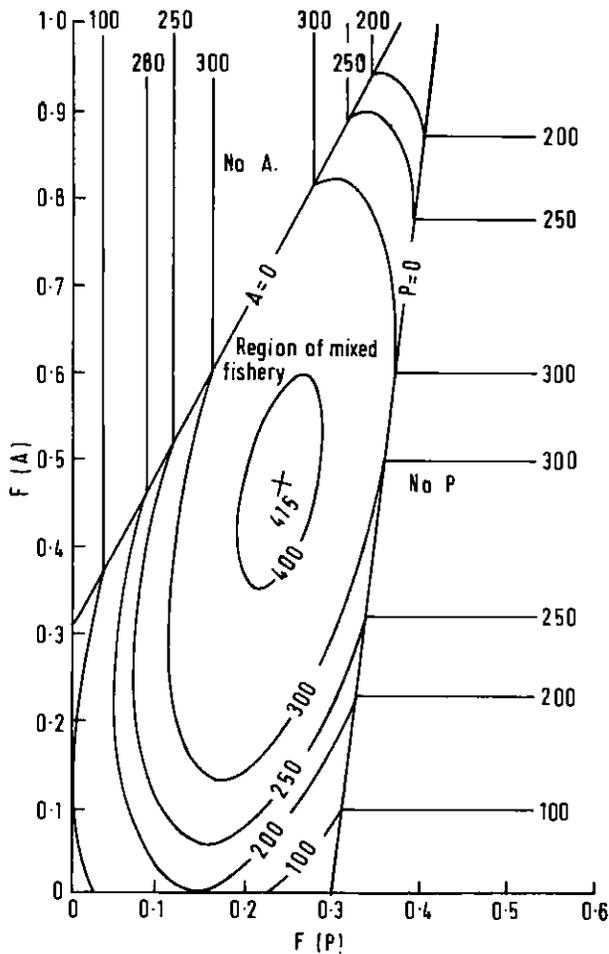


Fig. 3. A situation between the extremes of Fig. 1 and Fig. 2.

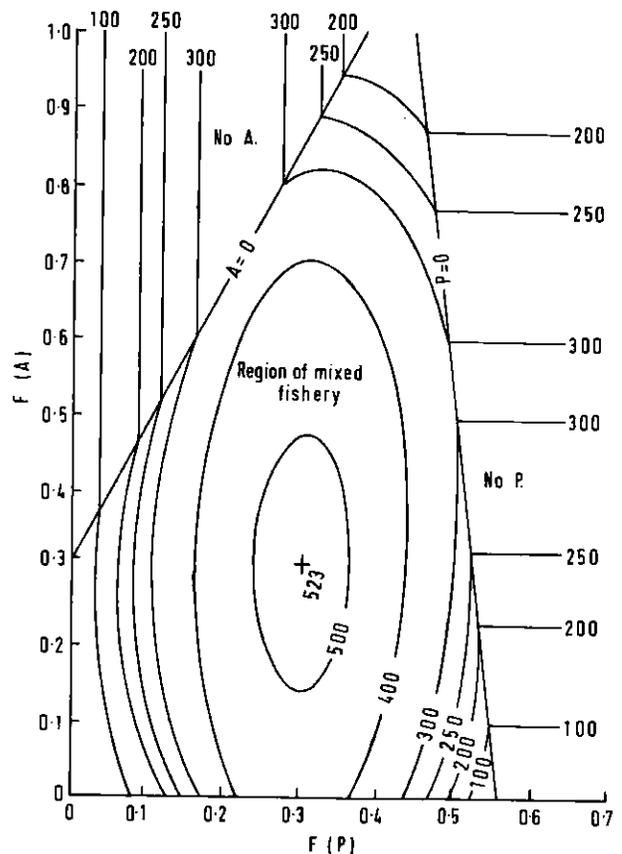


Fig. 4. As Fig. 1, but with the interaction terms numerically equivalent to those of Fig. 3 and the sign of the interaction of anchovy on pilchard reversed in order to examine a prey-predator type system.

If the by-catch rates in the various directed fisheries were not so large, the sector in which effort would cause fishing mortalities to be generated would be wider and the fishing mortalities generated on the two stocks could differ in proportion to a greater extent. Under these circumstances, a total effort quota would be less likely to generate a satisfactory management scheme unless it was backed up by individual stock catch quotas or effort quotas. If this were not done, there would be no guarantee that the proportion of the effort employed on the various stocks would in fact be that which generated the maximum yield. A study of Fig. 1 through 4 reveals that the proportion of mortality going on each stock effects both the total yield that can be achieved and also the level of effort at which it can be taken. As an example of this in the system examined in Fig. 2, if the proportion of $F(P)$ to $F(A)$ was 2 to 1, the maximum yield would be about 400,000 tons at a fishing mortality of approximately (0.230, 0.115). If, on the other hand, the proportion were in the ratio of 1 to 2, the maximum yield would be greater than 550,000 tons at fishing mortalities of approximately (0.25, 0.50). Thus the pro-

portion in which the mortalities are generated crucially affects both the total yield and the level of fishing effort which generates it. The history of fishing in the ICNAF Area does not lead one to suppose that fishermen could be relied upon to generate fishing efforts in the most advantageous proportion if the choice were left to them. If, on the other hand, catch or effort quotas for individual stocks are imposed, they define a unique position of the yield functions of Fig. 1 through 4, and consequently a total effort quota would only act as a safety net to prevent serious over-exploitation in the case of badly set stock quotas.

Similar criticisms to those made above also affect total catch quotas. A total catch quota might, however, be of some value in a highly interactive fishery such as that described in Fig. 1. In this case, a total catch quota might be expected to be successful but it would not guarantee that the species mixture in the catch was always the same. In fact, since presumably the most attractive species would sustain the highest mortality, it is possible that this would be overfished and the system move into a region where the total yield was similar but where it was composed of some less attractive species. In other words, if you want a fish meal fishery and you do not care what you catch, an overall catch quota on a highly interactive fishery might be successful. If, however, you wish to continue to catch prime fish, individual stock constraints are necessary.

The above criticism of total quotas assumes, however, that we have detailed knowledge about the nature of the interaction in the fisheries. If we do not, then a total effort quota or total catch quota would be a means of recognizing that the overall MSY of the system would be less than the sum of the individual stock MSYs, when either the fish stocks are interactive biologically or the by-catch rates in directed fisheries prevent the total MSY from being attained. In the former case biological considerations might suggest a likely level for the overall MSY and hence for the total catch quota. As a system of management, it would, however, have no scientific advantage over reducing the total allowable catch for each species to an appropriate proportion of the species MSY.

CONCLUSIONS

Considerations of mixed fishery models which include biological interactions lead to the conclusion that the total yield from an interactive system would be lower than the sum of the individual species MSYs. They do not lend support to the adoption of total catch or total effort quotas without individual stock constraints as a means of managing such systems. Such total quotas might, however, be of some value in taking account of the fact that the total MSY of a system might be less than the sum of the individual stock MSYs. Thus, they would be of greatest value where knowledge of the stocks was incomplete. However, the equivalent result could be achieved with greater safety and less complicated regulations by simply reducing the total allowable catches for the individual species by an appropriate proportion.

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The Application of Mixed Fisheries Theory to the Cod and Redfish Stocks of Subarea 2 and Division 3K

by

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INTRODUCTION

In Newfoundland 'fish' means cod unless otherwise stated which gives some indication of the importance of this species to the fisheries of the area. It has provided 80% of the catch of groundfish from Subarea 2 and Division 3K in the last 15 years. If the cod stock is in a depressed state, the total groundfish resources of the area must be depressed regardless of the strength or weakness of other species. Therefore, it is important to isolate the management need of the cod from those of the other groundfish. In doing this, however, it is necessary to ask whether there are any biological or fisheries interactions to consider with other species. Clearly, it is desirable that a mixed fishery model such as that developed by Pope (MS 1975) be applied, and that proposals for management regions be viewed in the light of the model.

THE APPLICATION OF THE SCHAEFER MODEL TO THE GROUND FISH OF SUBAREA 2 AND DIVISION 3K

Pinhorn (1976) found that the groundfish resources of Subarea 2 and Div. 3K exhibited catch per effort trends, which correlated significantly with the fishing effort adjusted by Gulland's method (Gulland, 1968) to allow for non-equilibrium effects. This was true for three separate units of fishing effort, and all three suggested that the overall maximum yield for groundfish was of the order of 400,000 metric tons. There was, however, some divergence between the three methods as to the precise cut back in effort which would be required to achieve this maximum sustainable yield. A unit of effort based on 901-1800 tons vessels of France, Portugal and Spain suggested a cut-back of 17% from the 1973 level of effort. A unit of effort based on vessels of the USSR and Poland of greater than 1,800 tons suggested that a cut-back of about 13% would be appropriate, while a unit of effort based on Spanish otter trawler (OT) cod catches suggested a cut-back of about 30%. At least part of this divergence is explained by the diversity of the various fleet objectives. The Spanish effort, which is based entirely on cod, shows the need for the greatest cut-back while the USSR and Polish effort, which is amongst the most diverse, shows the least. Another reason for the discrepancy is that only the Spanish effort is adjusted for seasonality, and, for that fleet at least, the tendency has been for catches to be made increasingly in the earlier months of the year when cod is most easily caught. The lack of such an adjustment for the other measures of effort might have masked the true increase in fishing effort in recent years. Against this point, it should be noted that the levels of fishing mortality estimated by virtual population analysis for the total cod stock in Div. 2J+3KL have not shown an increase in recent years similar to that displayed by the Spanish effort. This could be a result of either (a) the Spanish otter trawlers becoming older and less efficient, or (b) optimistically low values of fishing mortality being used to initiate the virtual population analysis. Whichever effort measure is used, it is clear from Pinhorn (1975) that all three measures suggest that the total groundfish catch per effort for Subarea 2 and Div. 3K can be represented by a Schaefer-type model. It is also clear that cod is by far the largest component of the groundfish resource, and it would therefore seem likely that cod would itself follow a Schaefer-type yield curve. Using the Spanish OT measure of effort from Pinhorn (1976) and regressing the resulting cod catch per effort on six-year running averages of the effort gives a significant linear regression; Fig. 1 shows the regression and the resulting yield curve. An alternative method of fitting the Schaefer yield function was suggested by Walter (MS 1975); it consists of regressing the catch per effort in year $i+1$ against the effort in year i . This method also gives a significant regression, and Fig. 2 shows this regression and the

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resulting yield curve. Gulland's method gives a MSY of 352,000 tons at an effort of 217,000 hours fishing, while Walter's method suggests a MSY of 417,000 tons at an effort of 263,000 hours fishing. Both methods suggest that the stock has been substantially overfished in recent years and that the 1973 level of effort needed cutting back by 32% in the former case, or by 18% in the latter case, in order to bring the stock back to the MSY level of exploitation.

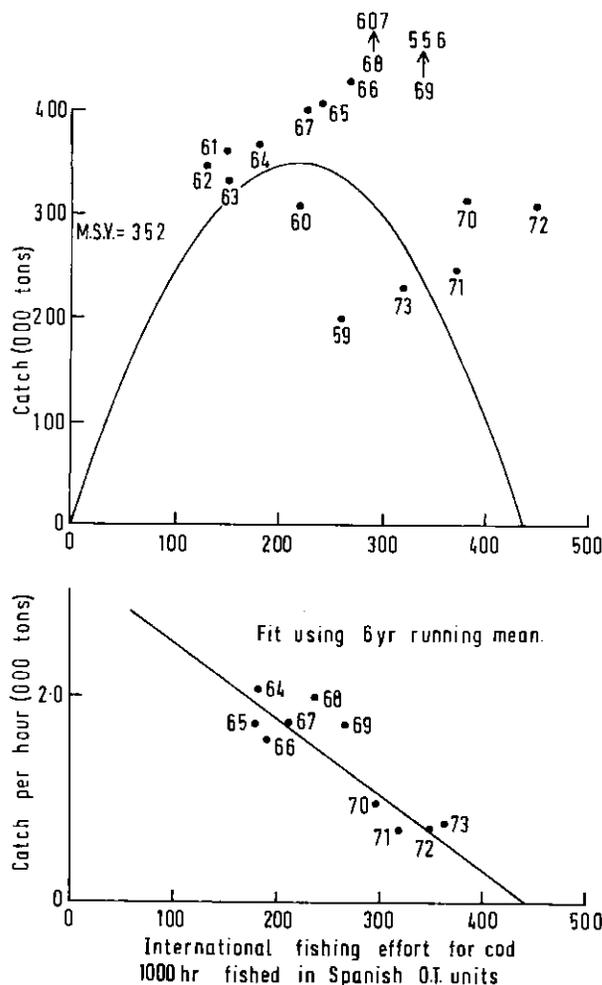


Fig. 1. Regression of cod catch per unit effort against a 6-year running average of effort and the resulting Schaefer-type yield curve, Subarea 2 and Div. 3K.

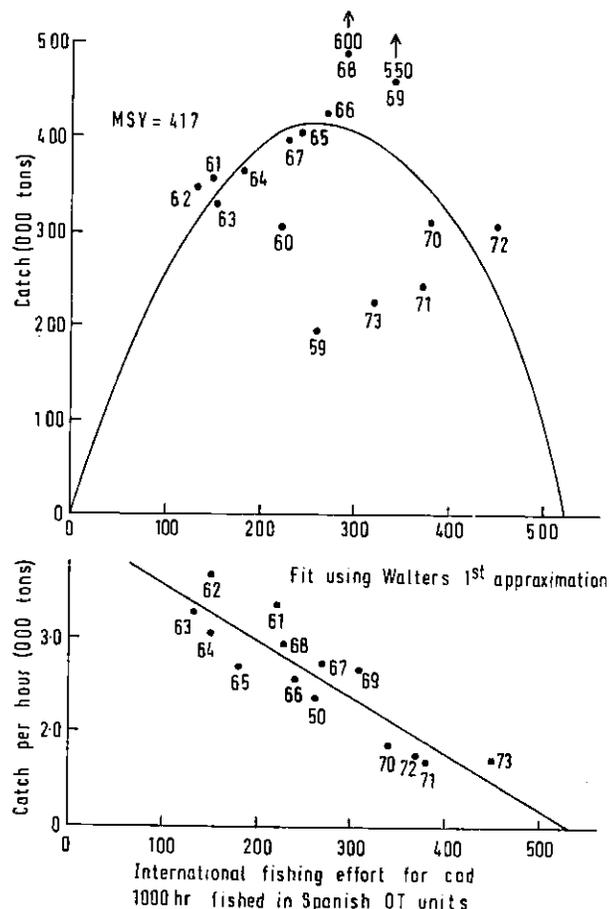


Fig. 2. Regression of cod catch per unit effort against fishing effort in the previous year (method of Walter (MS 1975), 1st approximation) and the resulting Schaefer-type yield curve, Subarea 2 and Div. 3K.

Apart from the cod, one of the other groundfish resources has also been shown to have a Schaefer-type yield curve: this is the redfish. Pinhorn and Parsons (MS 1974) derive several possible yield curves for this species, one of which is based on a six-year averaging period and has an equation governing its equilibrium behaviour of

$$R = 32.47 - 0.0056 fr \quad (1)$$

where R is the catch per effort of redfish, and fr is the fishing effort on redfish averaged over the last 6 years and is measured in standard days fished by vessels greater than 1,800 tons. Thus, two of the most important stocks of fish in the region appear to follow Schaefer-type yield curves. Since these stocks have accounted for 91% of the total catch in the period, it is not perhaps so surprising that the total groundfish catch appears to follow a Schaefer-type yield curve. Pope (MS 1975) points out that, where total effort develops in a constant ratio on two non-interacting fish stocks and both have parabolic yield functions, the resulting joint yield function on total effort

will also be parabolic. But the maximum yield it predicts need not necessarily be the true MSY of the system nor need the level of effort at which this apparent maximum yield is attained be the level of effort that applied correctly would give the true maximum yield of the system. Horwood (1976) suggests that the equilibrium development trajectory of a fishery need not necessarily pass through the overall MSY of such a system.

AN APPLICATION OF MIXED FISHERY THEORY TO THE COD AND REDFISH STOCKS OF SUBAREA 2 AND DIVISION 3K

Since both the cod and the redfish stocks of Subarea 2 and Div. 3K have yield curves that can possibly be represented by parabolas, the mixed fishery theory advanced by Pope (MS 1975) should be applicable, provided that there are no strong biological interactions between the species, for example, interactions of the type shown by Pope and Harris (MS 1975) for the South African pilchard and anchovy stocks and discussed in detail by Pope (1976). Attempts to improve the regressions for cod and for redfish using the catch rate of the other species as a second independent variable resulted in no significant co-efficients for this variable. It would thus seem that, if there are biological interactions between these two species, they are of a sufficiently low order to be ignored for practical purposes; consequently the total yield for the redfish and cod was calculated for different levels of fishing effort on the assumption that there are no interactions. Figure 3 shows the contours of equal yield in relation to the effort on both species.

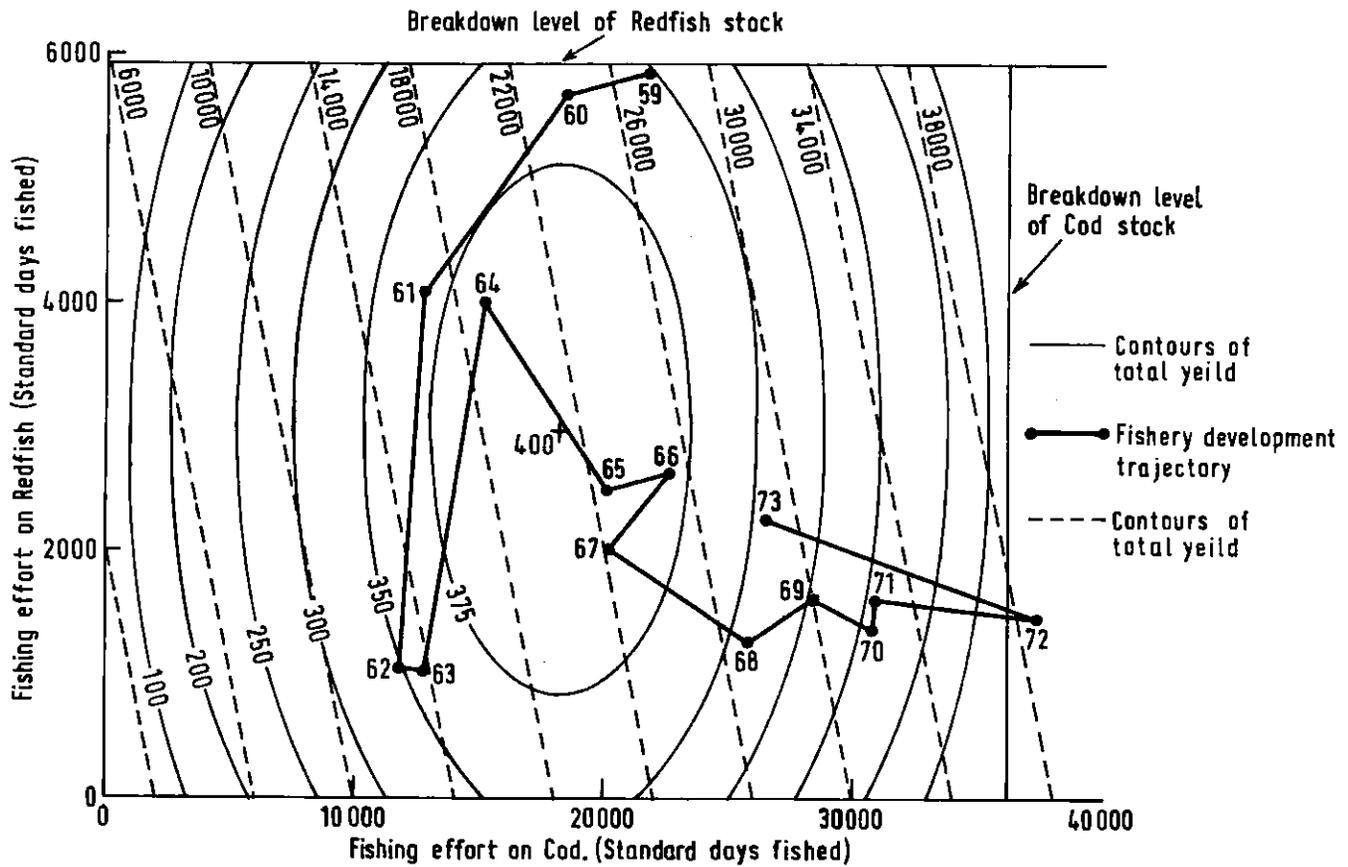


Fig. 3. Contours of total yield, contours of total effort (broken lines) and the development trajectory of the fishery for cod and redfish in Subarea 2 and Div. 3K.

The individual stock yield curves used to construct this joint stock function were (a) the yield curve of Pinhorn and Parsons (MS 1974) for the redfish, and (b) the yield curve developed for cod in the previous sections. In both cases the six-year running average method of fitting was used; this was adopted in order to choose the more pessimistic and therefore safer formulation and to remain consistent with the overall yield

function of Pinhorn (1976). The basis of the fishing effort used in the case of the cod was the hours fished by Spanish OT. In order to make it compatible with the standard days fished figure for the redfish, the "hours fished" effort has been divided by 12. This figure was chosen on the basis of a comparison of the cod catch rates in this region of USSR vessels greater than 1,800 tons with the Spanish OT catch rates. Thus the parallel diagonal lines in Fig. 3 show the levels of the total joint effort on the two species in standard days fished by vessels greater than 1,800 tons. The contours of equal total yield are concentric ellipses with their major and minor axis parallel to the co-ordinate axis. These indicate that the maximum yield for cod and redfish combined is of the order of 400,000 tons, attained at an overall fishing effort of about 21,500 standard days fishing. It is thus interesting that these two stocks alone exhibit the same MSY yield as that obtained from all groundfish species by Pinhorn (1976), particularly as similar measures of effort and averaging periods were used. This seems to bear out the suggestion of Pope (MS 1975) that the total yield obtained from assessments of total groundfish would tend to give lower bounds to the total maximum sustainable yield of a system. This becomes more believable when the development trajectory of these two fisheries is examined. It is superimposed on the yield function in Fig. 3 and shows that the proportions of fishing effort employed on these two fish stocks have fluctuated considerably in the period from 1959 to 1973. It is of course possible that, if the other groundfish resources of this region were strongly interactive with cod and redfish, then the figure of 400,000 tons for cod and redfish alone would be compatible with the 400,000 tons for all groundfish of Pinhorn (1976). This is because, in that case, the other groundfish species might have only increased in abundance after the cod and the redfish were depleted. This hypothesis is superficially tempting in the light of the figure 2 of Pinhorn (1976), which shows the proportion of other species in the catch increasing dramatically after 1969 when the cod and the redfish were both exhibiting low catch rates. Unfortunately, due to the lack of specific effort measures for these species in the area, this hypothesis cannot be tested directly. Nevertheless, the presence of older fish in significant quantities in the catch of several of the species of other groundfish; for example, roundnose grenadiers (Pinhorn, MS 1974) and Greenland halibut (Bowering and Pitt, MS 1975), suggests that they have not increased vastly in abundance in the recent past, and thus it is likely that they do not interact strongly with the cod or redfish. It is probable that the total groundfish MSY for this region is greater than the 400,000 tons joint maximum yield of the cod and redfish.

POSSIBILITIES FOR THE MANAGEMENT OF THE COD, REDFISH AND OTHER GROUND FISH STOCK COMPLEX IN SUBAREA 2 AND DIVISION 3K

Management of fish stocks in Subarea 2 and Div. 3K has until now been based on individual stock catch quotas designed to maximize the yield of each stock in isolation. In the light of the disturbing trends in catch rate shown by Pinhorn (1976) and indicated by groundfish survey results (ICNAF, 1975), it is certainly sensible to ask if other methods of management might be more appropriate. In particular, it is interesting to ask if either a total effort quota or a total catch quota would serve a useful purpose. Superficially, the use of an overall effort quota as the only management control in this region seems likely to be disastrous in the light of the volatility of the development trajectory shown in Fig. 3, and clearly such a constraint would seem unlikely to prevent heavy overfishing of redfish. For example, the overall level of effort in 1973 for cod was not much different from that in 1959, and also the situation in 1973 for cod was rather similar to that in 1959 (see for example Fig. 1). However, the redfish stock in 1959 was being exploited at the total destruction level of effort, while in 1973 the level of effort on it was rather below the MSY level. This is a feature of the much greater level of effort needed to attain MSY for cod (18,000 standard days) compared to that needed to attain MSY for redfish (about 3,000 standard days). The case with other species might well be rather similar, with a tendency for them to be heavily overfished if they became attractive to fishing effort; for example, as a result of a large year-class or a further decline in the catch rate of cod. In order to examine this management method more objectively a simulation was made of the cod and redfish fisheries, assuming that they followed the non-equilibrium form of the Schaefer curve

$$\frac{1}{P} \frac{dP}{dt} = b - aP - qf \quad (2)$$

where P is the stock biomass, t is time, f is the fishing effort and q the catchability coefficient. The parameters b and a and q were chosen to be consistent with the fitted yield curves, but, in order to provide the third parameter, it was necessary to assume the MSY level of fishing mortality. Consequently, an MSY for F = 0.2 was adopted for the redfish and an MSY for F = 0.3 for the cod. In order to be able to simulate the joint fishery for both species, it was assumed that the proportion of the total effort employed

on cod was given by

$$\frac{(v Cq)^n}{(v Cq)^n + (w R\hat{q})^n} \quad (3)$$

where n is some power, v and w are preference weightings for the cod and redfish respectively, C is the biomass of cod, R is the biomass of redfish, and q and \hat{q} are the respective catchabilities of the two species. This is analogous to the economic weightings used in the model by Clayden (1972) discussed by Garrod and Pope (1972). In order to acquire values of n, v and w, a regression of $\ln(fc/fr)$ on $\ln(c/r)$ was performed for the years 1959-73, where fc and fr were the effort applied to cod and redfish respectively in each year, and c and r were the recorded catches per effort of the two species. No significant regression emerged from this analysis and consequently, in order to be able to make a simulation, values of n = 2, v = 2 and w = 1 were adopted. A simulation based on these values was performed but, nor surprisingly, it did not reproduce the historical series, and the developmental trajectory it produced was far less volatile than the true series. In particular, the ratio of effort employed on redfish to that employed on cod was very much more regular than the ratio observed in the historic series (Table 1). This simulation was extended to show the possible behaviour of the mixed fishery under an overall effort quota (21,000 standard days) designed to achieve the MSY for the system. Table 2 shows the results from this simulation. It is apparent that the simulation settled down rapidly to a level of effort for the cod of about 17,000 days and a level of effort for the redfish of about 4,000. Fig. 3 indicates that, in the equilibrium case, this would achieve a joint yield in excess of 375,000 tons. In fact, the simulation finally settles down to a yield of 389,000 tons, a very substantial portion of the joint MSY of 400,000 tons. Thus, if the effort were distributed between stocks according to Equation (3) and the two stocks were precisely governed by the Schaefer equation and no other species affected the balance, then the total effort quota could be expected to quite successfully manage these two stocks. This is in line with Horwood's (1976) finding that such a system would tend to converge to some equilibrium level for the two stocks. In fact, of course, the model of fisheries preferences for species (Equation (3)) is at best a very poor fit to the facts and Schaefer curves very rarely fit a stock closely. Thus the equilibrium behaviour simulated would in practice tend to be disrupted by random events such as unusually large or small year-classes or changes in catchability. Clearly, a total effort quota might well be a good deal less efficient than the simulation in Table 2 would suggest.

Table 1. Simulation of the historic series for the cod and redfish stocks, Subarea 2 and Div. 3K.

Year	Historical levels of cod and redfish effort		Redfish as % of cod	Simulated levels of cod and redfish effort		Redfish as % of cod
	Cod	Redfish		Cod	Redfish	
1959	21,667	5,800	27	22,139	5,861	26
1960	18,333	5,700	31	19,530	4,470	23
1961	12,500	4,200	34	14,077	2,922	21
1962	10,830	1,100	10	10,907	2,092	19
1963	12,500	1,200	10	11,820	2,179	18
1964	15,000	4,200	28	16,011	2,989	19
1965	20,000	2,400	12	19,276	3,723	19
1966	22,500	2,800	12	20,885	4,115	20
1967	19,170	2,000	10	18,414	3,586	19
1968	25,830	1,400	5	22,613	4,387	19
1969	28,330	1,700	6	25,067	4,933	20
1970	31,670	1,400	4	26,709	5,291	20
1971	30,830	1,700	6	26,734	5,266	20
1972	37,500	1,600	4	32,524	6,476	20
1973	26,667	2,400	9	24,285	4,715	19

Table 2. Simulation of an overall effort quota from 1974 onwards. (Total effort is 210,000 standard days.)

Year	Total effort		Total yield
	Cod	Redfish	
1974	14,949	6,051	227,582
1975	15,915	5,085	260,324
1976	16,406	4,594	290,976
1977	16,654	4,346	316,071
1978	16,772	4,228	335,382
1979	16,819	4,181	349,758
1980	16,827	4,173	360,282
1981	16,816	4,184	367,939
1982	16,798	4,202	373,510
1983	16,778	4,222	377,580
1984	16,758	4,242	380,567
1985	16,741	4,259	382,772
1986	16,727	4,273	384,408
1987	16,716	4,284	385,627
1988	16,706	4,294	386,539
1989	16,699	4,301	387,223
1990	16,693	4,307	387,737
1991	16,689	4,311	388,124
1992	16,686	4,314	388,417
1993	16,683	4,317	388,637
1994	16,681	4,319	388,804
1995	16,680	4,320	388,930
1996	16,678	4,322	389,025
1997	16,678	4,322	389,098
1998	16,677	4,323	389,152
1999	16,676	4,324	389,193
2000	16,676	4,324	389,225
2001	16,676	4,324	389,248
2002	16,675	4,325	389,267
2003	16,675	4,325	389,280

Similar simulations were made of the effects of overall catch quotas. The levels of quota considered were 250,000 to 330,000 tons in 10,000 tons increments. The method of making these simulations was to divide each year into ten equal periods and simulate in each period the proportion of fishing effort being applied to each stock, according to Equation (3). Fishing was stopped at the end of the time period in which the catch quota was exceeded. This method of simulating a catch quota invariably led to the quota being exceeded, in some cases by amounts in excess of 10%. (Thus accidentally adding verisimilitude to the simulation.) A total effort constraint of 30,000 days was put into the simulation to avoid quotas being taken by improbably high levels of fishing effort. All of the quotas over 310,000 tons eventually came up against this constraint, implying that they would lead to overfishing of the two stocks if applied at present. It would however be possible to bring total catch quotas up to some higher level at a later time if the stocks were first allowed to rebuild at the lower quota levels. The simulations showed the same well-behaved distribution of fishing effort observed for the effort quota simulation. Since this was achieved under the same model assumptions, this simulated behaviour is open to the same criticisms as were levelled at effort quotas. A third possibility for management would be a stock constraint. This would imply reducing fishing until the cod catch rate increased to 1.62 tons per Spanish OT hour and until the catch rate of redfish increased to 16.24 tons per standard day fished. This would imply resting the cod for about 2 years or fishing at an effort level below MSY for a longer period. The catch rate of redfish is currently at about this level.

DISCUSSION

The Schaefer curves fitted to the cod for Subarea 2 and Div. 3K suggest that this fish stock has been very seriously overfished in recent years. The overall yield function for redfish and cod suggests that the estimate given by Pinhorn (1976) of 400,000 tons as the maximum yield for the total groundfish resources of this region may be somewhat pessimistic, but it still implies that the 1973 level of fishing effort on these two stocks needs reducing by about 28%. The lack of observable biological interaction between these

two stocks, and indeed the other groundfish stocks, suggests that there is no biological reason why individual stock catch quotas should not be successful provided they are set at the right level.

A study of the development trajectory in Fig. 3 suggests that the directed fisheries for these two species are sufficiently pure (i.e. have low by-catch rates) to include the joint MSY levels of effort in a region that is attainable. Thus, the possible arguments relating to the overall attainable MSY of a system being lower than the joint MSY, advanced by Pope (MS 1975), are not valid in this case. While the overall MSY is attainable in the long-term equilibrium sense, simulations of a total catch quota suggest that such a quota or the sum of the two species quotas should be set well below the MSY level of 400,000 tons due to the present depleted state of the cod stock.

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The Influence of Fluctuations in Recruitment on Fisheries Management Strategy, with Special Reference to Southern Gulf of St. Lawrence Cod

by

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ABSTRACT

Adult stock biomass has been demonstrated to be more important than environmental fluctuations in determining year-class size of southern Gulf of St. Lawrence cod. The coarse tuning of recruitment is achieved by the response of egg production to changes in the growth rate of the adult stock. Fine tuning results from the predation of adult cod on juveniles after they enter the demersal phase. A possible mechanism tending to produce a constant L_1 length is discussed as a stabilizing factor on the biomass of the total stock. The most stable and productive level at which to maintain the adult stock biomass is 150,000 metric tons. This gives the maximum acceleration of growth in response to perturbations in stock biomass since it is at the point of inflection of the relationship between stock biomass and growth rate.

Cycles and fluctuations in recruitment due to the lag time between spawning and recruitment and environmental fluctuations, respectively, proved to be the most important factors in determining the relative merits of different management strategies. Management by constant catch quotas was the poorest strategy considered, resulting in large fluctuations in stock size and fishing effort and leading to a collapse of the stock at lower levels of exploitation than could be maintained by other strategies. Catch quota regulation accentuated the natural cyclic variation of an unfished stock by relating fishing effort inversely to stock biomass. Controlling the fishing mortality rate (constant effort quotas) opposed the natural cyclic tendency of the stock resulting in stability of catch and stock biomass and high levels of yield. Simulation results indicate that control of the spawning stock biomass at 150,000 tons results in high average catches while biomass control at levels of 120,000 or 170,000 tons results in fluctuating catches. At low levels of fishing mortality, biomass control appears to produce higher yields with slightly less fluctuation in yield than effort control with the same average biomass.

Yield is increased by allocating more effort to the summer fishery than to the winter fishery. This is due to reduced predation of adults on juveniles and increased stability of spawning stock size. The winter fishery removes age 3 fish before they can spawn.

The relation between fishing effort and yield in the model may be described as one half of a Schaefer yield curve, rising quadratically as F increases from zero and dropping discontinuously from the peak to zero at high levels of F due to recruitment failure. Yield per recruit calculations involving levels of F greater than 0.5 are not a satisfactory basis for management due to the risk of recruitment failure.

It is recommended that the southern Gulf of St. Lawrence cod stock be managed by maintaining the adult stock biomass near 150,000 tons. The yield of 40,000-50,000 tons, representing P/B ratio of 0.6, may be achieved through biomass or effort control with $F = 0.4$.

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INTRODUCTION

Historically, fisheries biologists, guided by such forerunners as Parrish and Jones (1953), Beverton and Holt (1957), and Ricker (1958) have rigorously studied the response of fish populations to exploitation, assuming constant recruitment independent of environmental effects. It has also been realized that the environment does play an important role in determining recruitment but the mechanism remains to be elucidated. In the light of the accepted importance placed upon these effects, egg and larval surveys were initiated in the southern Gulf of St. Lawrence to link up environmental effects on recruitment with those due to fluctuations in parent stock biomass.

The Atlantic cod (*Gadus morhua* L.) stock, of primary interest in this paper, has been shown to occupy only ICNAF Division 4T and Subdivision 4Vn on the basis of three tagging studies (McCracken, 1959; Martin and Jean, 1964; Kohler, MS 1975). During the autumn, cod age 4 and older emigrate from the southern Gulf and overwinter on the edge of the Laurentian Channel east of Cape Breton. In May, they again migrate to spawn in the highly productive shallows of the southern Gulf (Paloheimo and Kohler, 1968). This stock supports two fisheries, a winter component off Cape Breton, and a summer component in the southern Gulf of St. Lawrence. Increases in fishing effort are usually reflected in catches from the winter fishery, while fishing effort has remained relatively constant in the summer in the southern Gulf of St. Lawrence.

This paper attempts to analyze the effect of temperature, as the key environmental factor, with parent stock biomass as the forcing functions of the stock recruitment mechanism for cod. The implications of these fluctuations in recruitment will be examined in relation to fisheries management strategy. The different management policies to be examined are the control of fishing effort, spawning stock biomass and catch.

METHODS

Data collections and amalgamation are discussed by Lett *et al.* These data were analyzed by response surface techniques (Cochran and Cox, 1968) to determine the relationship among the dependent and independent variables. The fitting procedure employed either a linear polynomial

$$Y = b_0X_0 + b_1X_1 + b_2X_2 + b_{11}X_1^2 + b_{22}X_2^2 + b_{12}X_1X_2$$

or the corresponding intrinsically linear model. The whole model was fitted using stepwise regression (Draper and Smith, 1966) and the equation was accepted based on the minimization of the error mean square.

DERIVATION OF EQUATIONS

Sea surface temperature (T_p) and estimated parent stock size (B) were found to be major factors affecting the catch of cod eggs (Eg) by survey during May (Fig. 1). The general relationships among these variables were described by the following intrinsically linear model:

$$\sqrt{\log(Eg+1)} = 3.876B - 1.7033B^2 + 0.7444T_p - 0.0595T_p^2 - 3.4005. \quad (1)$$

Variable	Coefficient	Standard error	Partial correlation coefficient
B	3.8786	0.6966	0.9411
B ²	-1.7033	0.2888	-0.9470
T _p	0.7444	0.4344	0.6506
T _p ²	-0.0595	0.0385	-0.7118

The coefficient of multiple determination (R^2) was 0.930, while F for regression was significant at 13.3 ($F_{.05} = 6.4$). The addition of T_p^2 resulted in neither T_p nor T_p^2 being significant along; however, there was a substantial drop in the error mean square and a 5% rise in the coefficient of multiple determination. Thus, the second order effect can be considered a significant variable (Draper and Smith, 1966). The variables used in Equation (1) are defined as follows:

Eg = the catch of eggs per 1000 m³ of water strained;

B = the estimated stock biomass ($\times 10^{-5}$) on May 1 for individuals aged 4 and older;
and

T_p = the mean sea surface temperature at Grande Rivière on May 20.

The sea surface temperatures taken on egg and larval cruises were well correlated with those at Grande Rivière ($r = 0.77$) on the western shore of the southern Gulf of St. Lawrence (Lauzier, 1969), and, consequently, the latter were used in the model to avoid the variance problems associated with predicting cruise temperatures using the annual Grande Rivière cycle.

In estimating the parent stock biomass, cohort analysis (Pope, 1972) was used to estimate the numbers of cod present in the parent population on January 1. The number of fish caught between January and May in ICNAF Div. 4T and Subdiv. 4Vn and the number lost to natural mortality ($M = 0.2$) (Clayden, 1972; Halliday, 1972) were subtracted from the January 1 estimate to give the size of the spawning population. Mean weights for each age were determined from commercial sampling data and multiplied by the corresponding numbers at age to give the parent stock biomass.

The abundance of eggs was found to decrease in relation to the second order effect of time (Lett *et al*, 1975a) and a correction was made using the linear model:

$$Eg = 11.6303B - 5.3270B^2 + 0.0297T_p^2 - 0.0039T_m^2 - 2.4256 \quad (2)$$

where T_m = the number of days to the midpoint of a cruise since May 1. For comparison, the egg abundance levels were all corrected to May 20 facilitating the elucidation of the true partial correlations of temperature and biomass. Peak spawning of cod is thought to occur between 3° and 5°C (Hjort, 1919; Bigelow and Schroeder, 1953) and the initiation of spawning was assumed to vary little from year to year in accord with Cushing's (1969) hypothesis. Spring bottom temperatures in the Gulf of St. Lawrence have remained remarkably uniform; therefore, May 20 represents some point on the egg production cycle which varies little annually, and represents the abundance of Stage II eggs.

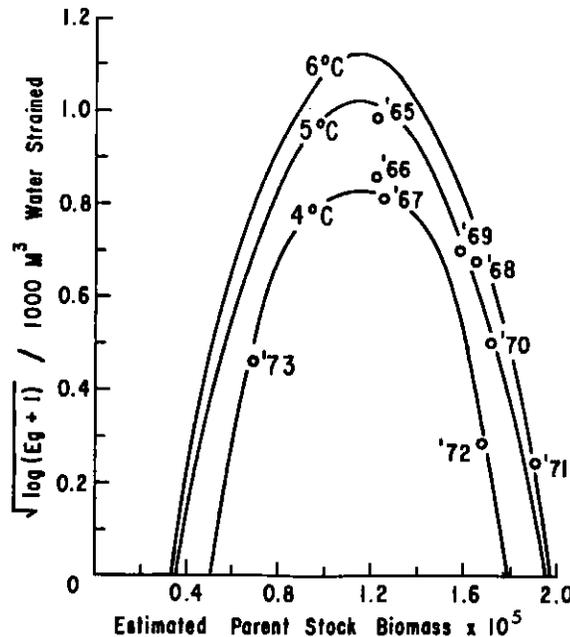


Fig. 1. Effect of estimated spawning stock biomass and temperature on the catch of cod eggs/1000 m³ of water strained. Points have been adjusted to estimate the abundance level on May 20.

The quadratic nature of parent stock biomass (Equation (1)) suggests a density-dependent mechanism is controlling the number of eggs (Fig. 1). The general trend over the data series is a decline in egg numbers with increasing stock biomass; however, in 1973 stock biomass was so low that a reciprocal response was observed. There are a number of possible explanations. However, the analysis suggests that either large estimated parent stock biomasses are producing fewer eggs or that large numbers of these eggs are dying immediately following spawning, since the mortality generated over time does not interact with parent stock biomass (Lett *et al*, 1975a).

The effect of temperature is also quadratic, although the β -coefficients indicate that only 32% of the total explained variation is attributable to temperature. The survival of cod eggs can be fitted to an optimum temperature of 6.25°C ($\partial/\log(Eg+1)/\partial T_p = 0$) in accord with the findings of Forrester and Alderdice (1966) and Bonnet (1939).

The abundance of cod larvae (L_R) was found to be positively correlated with the catches of cod eggs (Eg) on May 20 but negatively correlated with time (T_m) (Fig. 2A). The following intrinsically linear model described the relationship among the dependent and independent variables:

$$\log(L_R+1) = [3.1527 \log T_p \times \log(Eg+1)] - [0.9709 \log T_m \times \log(Eg+1)] - 0.0244. \quad (3)$$

Variable	Coefficient	Standard error	Partial correlation coefficient
$\log T_p \times \log(Eg+1)$	3.1527	1.7741	0.4420
$\log T_m \times \log(Eg+1)$	-0.9709	1.0024	-0.2594

The coefficient of multiple determination (R^2) is 0.76 while F for regression is significant at 12.31 ($F_{0.5} = 4.5$), where L_R is the catch of larvae per 100,000 m³ of water strained, Eg is the catch of eggs per 1,000 m³ of water strained (adjusted to May 20), and T_p is the annual mean monthly maximum sea temperature at Grande Rivière. The effect of the time \times egg interaction is rather inconclusive, suggesting that the loss rate (Fig. 2A) is not large for cod larvae in relation to the accuracy of abundance measurements over the time series analyzed. Density-dependent mortality at the larval stage is of marginal importance in determining the final number of metamorphosis, which is in accord with Hemple's (1965) hypothesis and our own findings for Atlantic herring (*Clupea harengus*) but in sharp contrast with our findings for Atlantic mackerel (*Scomber scombrus*) (Lett *et al*, MS 1975c). As the temperature increased, the survival of cod larvae increased exponentially, as found by Hermann *et al* (1965) for cod larvae at West Greenland.

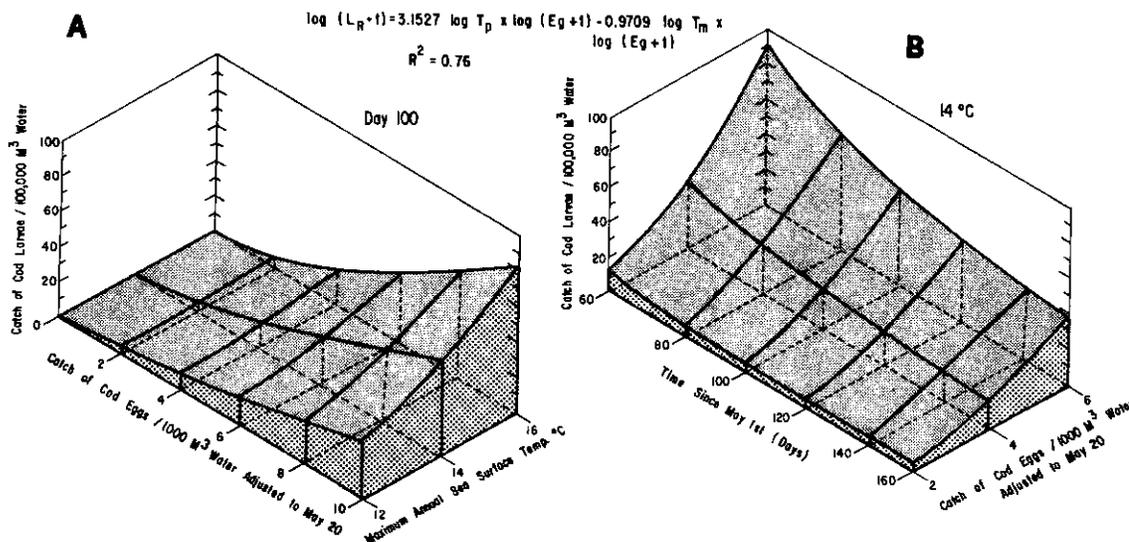


Fig. 2. Effect of time, temperature, and egg abundance on the catch of cod larvae/100,000 m³ of water strained. The egg abundance are those adjusted to May 20.

Equations (1) and (3) were used to predict the numbers of larvae on July 20 for the particular stock biomasses and temperatures which existed in the years 1963-1970. These larval abundance levels were then compared with the year-class sizes from cohort analysis and stock biomasses 2 years later, using the following intrinsically linear multivariate relationship. The equation was forced to approach zero when there were no larvae.

$$\log \left(\frac{Y_{\max} - Y_R}{Y_R} \right) = -6.1121(\log L_R) + 1.1675(\log L_R)^2 + (0.7131B \times L_R) + 2.9320. \quad (4)$$

Variable	Coefficient	Standard error	Partial correlation coefficient
$\log L_R$	-6.1121	1.0710	-0.8959
$(\log L_R)^2$	1.1675	0.2497	0.8555
$B \times \log L_R$	0.7131	0.2929	0.6523

The coefficient of multiple determination (R^2) is 0.87, while F for regression is 11.32 ($F_{0.5} = 5.4$), where Y_{\max} (130,000) is the maximum year-class strength observed since 1960 and is assumed to represent an asymptotic year-class strength as long as the total pelagic biomass (herring and mackerel) remains relatively constant.

However, B in Equation (4) represents the biomass of adult cod 4 years and older. The relationship of adult cod biomass and year-class strength is sigmoid and negatively correlated (Fig. 3) as a result of the younger cod having to fit into a productive constraint on the adult cod biomass. The dependence of year-class strength on the number of larvae (L_R) is log normal with the ascending limb of the curve being density dependent (i.e. cannibalism (Ricker 1954)) as well as the descending limb. This effect is demonstrated by the $L_R \times B$ interaction. Equation (4) can be transformed to a non-linear form.

$$Y_R = \frac{Y_{\max}}{1 + \text{antilog}[-6.112(\log L_R) + 1.675(\log L_R)^2 + (0.713B \times \log L_R) + 2.934]} \quad (5)$$

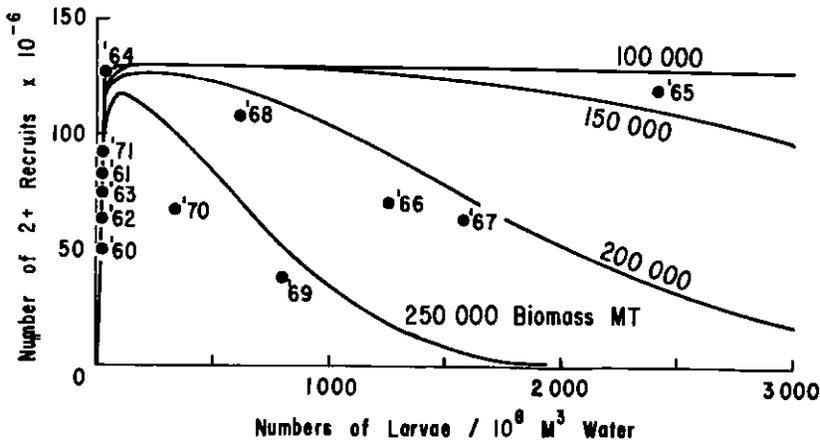


Fig. 3. Effect of the interaction of larval abundance and stock biomass of cod age 4 and older on the recruitment of juvenile cod age 2+. Individual points were predicted using Equations (1) and (3) for a larval abundance level on July 20. Only the data series from 1963 to 1971 was used in determining the relationship.

MODEL STRUCTURE

A system simulation (Fig. 4) was constructed combining the structural equations relating biomass to growth and numbers of age 2+ recruits and biomass and temperature to egg and larval numbers with an estimated selection ogive for 4½-inch mesh otter trawl nets

to allow the long-term effects of various management strategies on the southern Gulf of St. Lawrence cod stock to be examined.

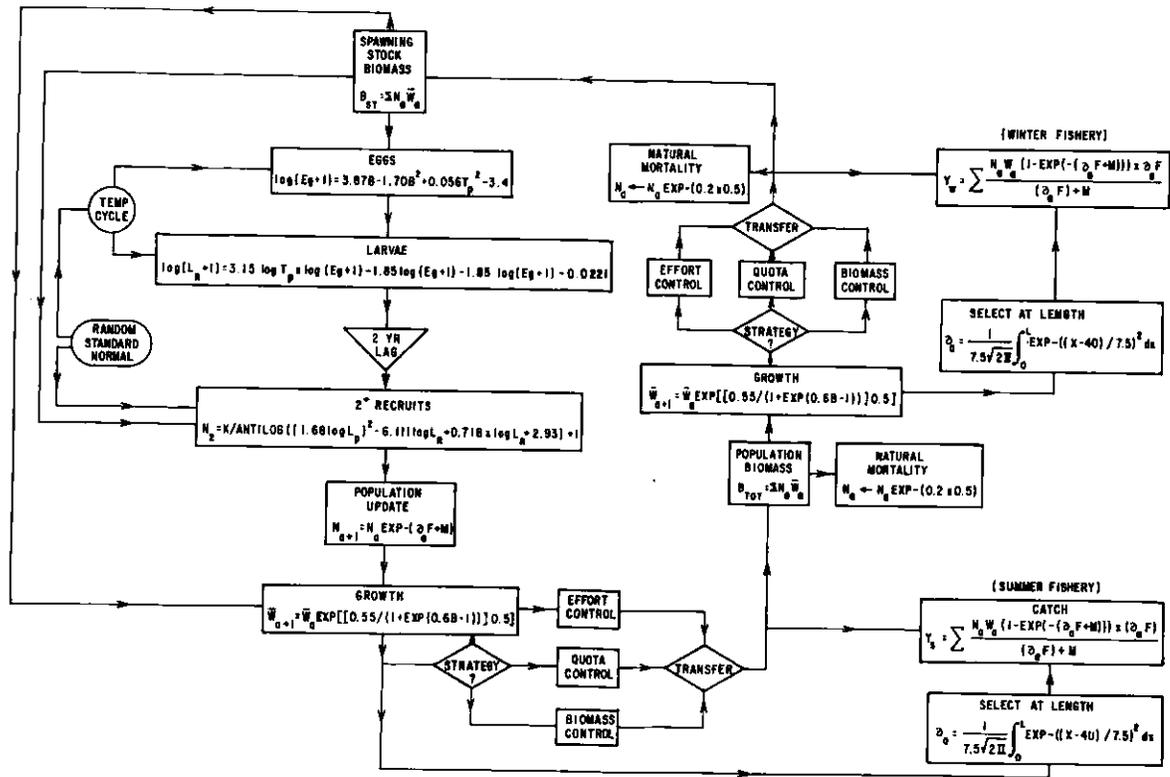


Fig. 4. A systems flow chart of the basic cod production system. The model allows for three kinds of management control: (1) effort control, (2) quota control, and (3) biomass control. A normally distributed random number sequence was added to the simulation to simulate the empirical effects of a random environment. Selection is by length.

The simulation was initialized by entering numbers at age N_a and mean weights (kg) at age W_a for ages 3-16 and selecting a level of fishing mortality for the summer fishery and a level of fishing mortality or a spawning stock biomass or a catch quota for the winter fishery. After initialization, the population biomass for ages 4-16 was calculated by the formula

$$B_{TOT} = \sum N_a W_a \times 10^{-8}.$$

This biomass determines the pre-winter growth rate for ages 3-16 and, together with larval numbers, the number of age 2+ recruits. The growth equation used is

$$W_a \exp\left\{0.5 \left(\frac{0.55}{1 + \exp(0.6B_{TOT} - 1)} \right)\right\} \rightarrow W_a. \quad (6)$$

Growth occurs twice annually in the model - before the summer and winter fisheries.

If the option of catch quota control or spawning stock biomass control was selected, then a level of F was estimated immediately prior to the winter fishery so that the desired catch or stock biomass subsequent to the winter fishery was obtained. Due to computing speed limitations of the machine used to implement the model, an approximation ignoring the shift in selection at age due to changes in growth rate was employed, so that catch or biomass was controlled within narrow limits. Under biomass regulation, if the stock biomass before the winter fishery was less than the required level, F was set to zero.

Selections at age factors (∂_a) were calculated for each fishery by transforming mean weight at age (W_a) to length at age (L_a) using a weight-length key

$$L_a \text{ (cm)} = \text{antilog} \left(\frac{\log W_a + 5.16}{3.05} \right) \quad (7)$$

based on keys derived for southern Gulf of St. Lawrence cod by Kohler *et al* (1970). The selection ogive was the cumulative distribution function of a normally distributed random variable with mean 40 cm and standard deviation 7.5 cm derived from data in Holden(ed), 1971.

$$\partial_a = \frac{1}{7.5\sqrt{2\pi}} \int_0^{L_a} \exp(-[(x-40).7.5]^2) dx. \quad (8)$$

In both the summer and winter fisheries, the standard catch equation (Beverton and Holt, 1957) with a semi-annual natural mortality of 0.1 was used.

$$y = \frac{\sum N_a W_a \partial_a F [1 - \exp(-[\partial_a F + 0.1])]}{\partial_a F + M} \quad (9)$$

Following each fishery, the numbers at ages 3-16 were reduced by the catch at age and one-half of the annual natural mortality by the relation

$$N_a \exp(-(\partial_a F + 0.1)) + N_a. \quad (10)$$

The update of numbers at age and weight at age occurred after the winter fishery and immediately before the calculation of spawning stock biomass. A total mortality rate of 0.2 was applied to age 2+ recruits and a weight at age 2+ of 0.3 kg was assumed.

The spawning stock biomass (ages 4-16) was calculated as

$$B_{SS} = \sum N_a W_a \times 10^{-8}. \quad (11)$$

Egg production was then calculated as $C \cdot |C|$ where

$$C = \sqrt{\log(\text{Eg}+1)} = 3.87B_{SS} - 1.7033B_{SS}^2 + 1.744T_p - 0.595T_p^2 - 3.4005 \quad (12)$$

where T_p was a random normal deviate with mean 5.01 and standard deviation 1.11, based on observed sea surface temperatures at Grande Rivière. $\log(\text{Eg}+1)$ was constrained to be non-negative.

The number of eggs was combined with a second random temperature deviate, independent of the first and normally distributed with mean 14.39 and standard deviation 1.28, derived from mean monthly maximum sea surface temperatures at Grande Rivière to calculate a number of larvae using the equation:

$$\log(L_R+1) = [3.15 \log T_p \times \log(\text{Eg}+1)] - [1.85 \log(\text{Eg}+1)] - 0.0244. \quad (13)$$

Temperatures in May were uncorrelated with the monthly maximum, usually occurring in August. Grande Rivière temperatures in May (Lauzier, 1969) had a correlation of $r = 0.77$ with those collected on plankton cruises. The number of larvae was used to determine the number of age 2+ fish 2 years later.

The number of age 2+ recruits was calculated using the population biomass B_{TOT} prior to the previous winter fishery and the number of larvae two years previous according to the relation

$$N_2 = \frac{X \times 130 \times 10^6}{1 + \text{antilog}[1.68(\log L_R)^2 - 6.11(\log L_R) + (0.71B_{TOT} \times \log L_R) + 2.93]} \quad (14)$$

where X is a random variable whose natural logarithm is normally distributed with mean 0 and standard deviation 0.1. The random multiplier X was introduced in the calculation of age 2+ recruits because 13% of the observed variance in recruitment was unexplained by the regression equation, and ignoring this residual variation results in spurious stability of recruitment at extreme levels of biomass.

Growth was applied to weight at age for ages 3-16 prior to the summer fishery using the same formula as before the winter fishery with B_{SS} substituted for B_{TOT} . The summer fishery was carried out at a preset level of F . The mesh selection calculations and catch equation were the same as for the winter fishery.

Following the summer fishery, the numbers at age were reduced by the formula

$$N_a \exp[-(\partial_a F + 0.1)] + N_a \quad (15)$$

and the yearly cycle of events began again with the calculation of B_{TOT} .

In this model, each year is divided into two intervals corresponding to the two fisheries with a semi-annual mortality rate of 0.1 applied to each interval. Growth rates and, through them, selection at age factors respond on a semi-annual basis to changes in stock biomass.

THE BIOLOGICAL BASIS OF THE MODEL

The abundance of cod eggs is directly related to the growth rate of the adult stock (Fig. 5) and may be still better explained by the production of the adult cod, $P = N(\Delta w/\Delta t)$. Through histological and gross analysis, Woodhead and Woodhead (1965) noted that, for cod, the number of ovarian follicles varies little; however, vitellogenesis does not occur in all eggs produced. There is a minimum number of mature eggs produced and any increase over this level is related to the growth rate of the cod. They go on to say that eggs not matured are reabsorbed. This mechanism was hypothesized by Lett *et al* (1975a) for Gulf of St. Lawrence cod.

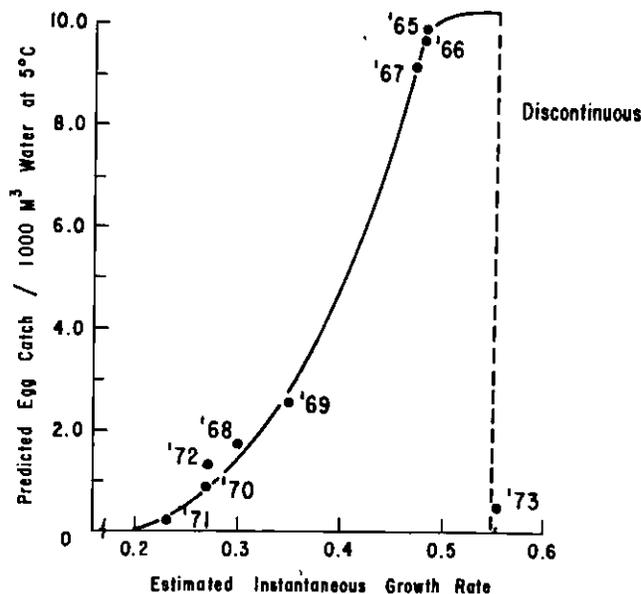


Fig. 5. Correspondence of the instantaneous growth rate with production of cod eggs. When the upper asymptotic growth rate is reached, the population is producing the maximum amount of gonad. The predicted number of eggs was on May 20 at 5°C, while instantaneous growth rate was estimated from its relationship with biomass.

It would seem that the growth rate, then, is providing the homeostatic core of the recruitment mechanism. Furthermore, it can be hypothesized that growth rate is a determining variable controlling the entire dynamics of the cod population. The annual abundance of 7-9 mm herring larvae is determined by herring production (Fig. 6), when environmental effects are removed. These results are not surprising in light of the work by Scott (1962) and Tyler and Dunn (1975). They found that the fecundity of rainbow trout (*Salmo gairdneri*) and winter flounder (*Pseudopleuronectes americanus*) was positively and linearly related to ration size (Fig. 7A). A threefold decline in ovary weight in relation to a twofold reduction in ration was due to a decline in the number of yolk bearing oocytes (Fig. 7B), this decline caused by a suppression in vitellogenesis and reabsorption of yolkless oocytes (Tyler and Dunn, 1975). Bagenal (1966) related changes in the fecundity of plaice to an increase in the availability of food due to a reduction in the population biomass. He went on to conclude that the fecundity of the population is modified by food availability,

and that fecundity acts as a density-dependent population regulatory mechanism. The same sort of density-dependent egg production mechanism has been noted for Atlantic mackerel (*Scomber scombrus*) (Lett *et al.*, MS 1975b), North Sea plaice (*Pleuronectes platessa* L.) (P.F. Lett, D. Harding, and R.C.A. Bannister, unpublished data), for *Esox lucius* L. (Kippling and Frost, 1969), and brown trout (*Salmo trutta*) (Bagenal, 1969). The second order relationship between egg production and stock biomass (Fig. 1) is only feasible when there is also density-dependent growth. For Gulf of St. Lawrence cod stock, the relationship between parent stock biomass and the instantaneous growth rate is clearly demonstrated (Fig. 8). For North Sea plaice, this relationship is not as lucid; however, it does exist (Bannister, 1975), which disagrees with Cushing's (1975a) hypothesis and the basic premise of the Beverton and Holt (1957) yield per recruit model. Using multi-variate techniques, no changes in the growth rate of Gulf of St. Lawrence Atlantic herring aged 2 and older could be attributed to changes in the biomass. The factors found to explain 89% of the changes in growth rate were temperature, the abundance of juvenile mackerel and the interaction of age \times temperature. This outcome suggests a basic difference between the recruitment mechanisms of herring and the two demersal species. However, in both cod and herring, egg production is closely linked to the growth rate.

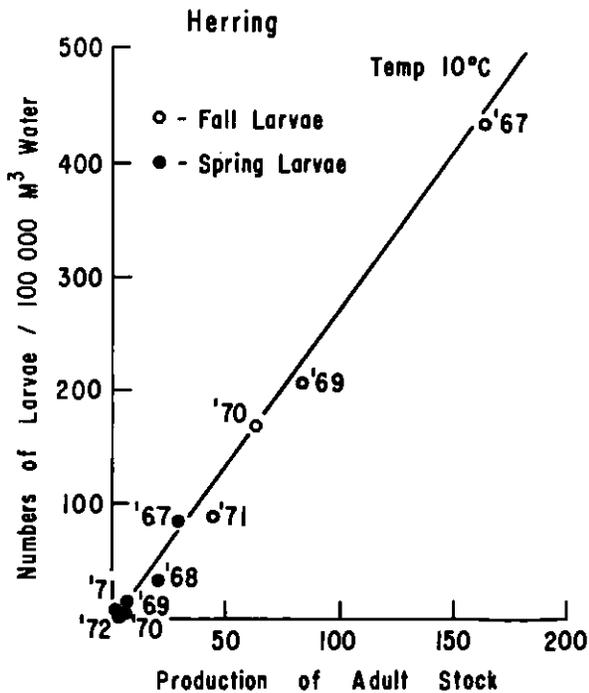


Fig. 6. The correlation between the number of 7-9 mm larvae and the cumulative production of adult stock. The points are all adjusted to 10°C. The relationship between cumulative growth rate and larval abundance is the same for both spring and autumn spawned larvae.

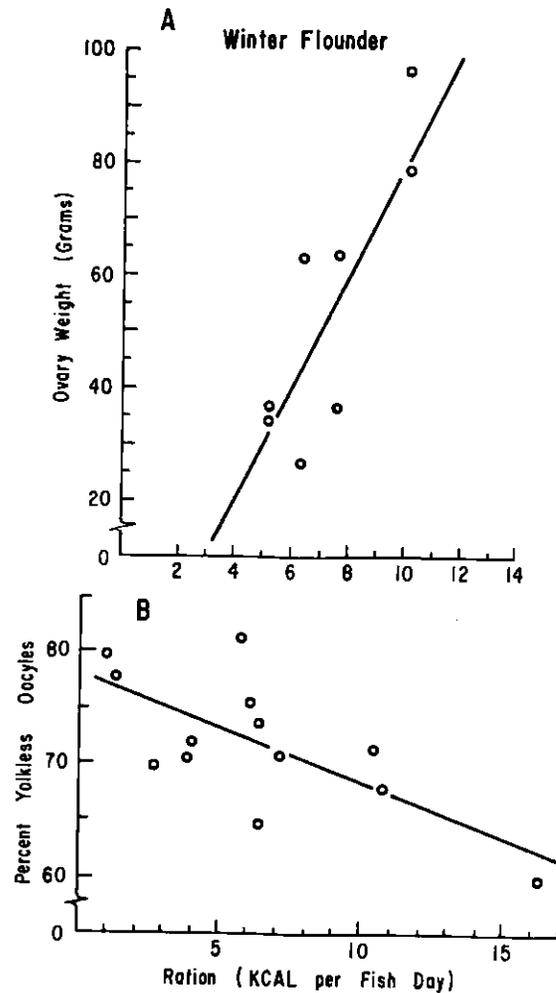


Fig. 7. Reproduced from Tyler and Dunn (1975), showing an increase in gonad weight with increasing ration size (7A), and a drop in the number of yolkless oocytes (7B).

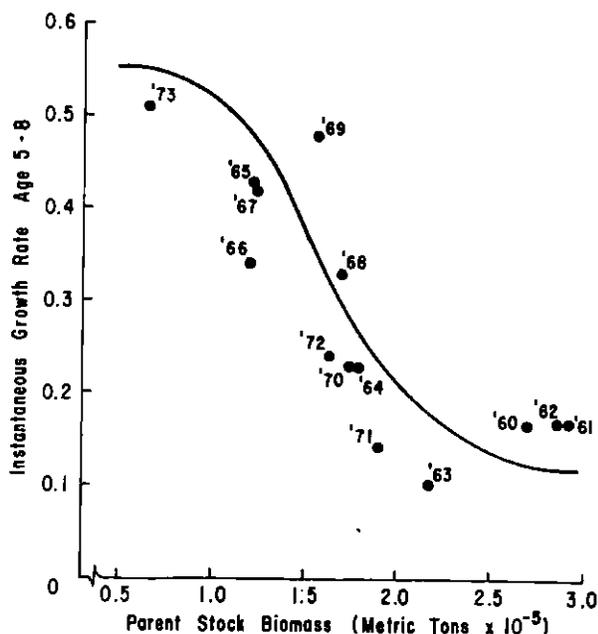


Fig. 8. Relationship between the summer biomass and the instantaneous growth rate of southern Gulf of St. Lawrence cod. The point of inflection of the curve occurs at about 150,000 tons.

The number of cod eggs caught on research cruises increases with temperature due to improved survival. Forrester and Alderdice (1966) indicated that both Atlantic and Pacific cod have an optimum temperature for the survival of eggs near 7.1°C for salinities similar to those observed in the Gulf of St. Lawrence. Bonnet (1939) shows similar results: with salinity of 32.31‰, egg production is maximized at 6.5°C.

As the number of cod eggs increases, the number of larvae also increases; furthermore, this increase is exponential (Fig. 2). The suggestion is that faster-growing, better-conditioned fish will produce more eggs (Fig. 5 and 6) and also more viable eggs (Fig. 7B) (Nikolsky, 1969; Tyler and Dunn, 1975).

The survival of cod larvae seems to be weakly density-dependent (Fig. 2B) with the final number being almost constant no matter what the initial number. However, metamorphosis would occur before this limiting value could be reached. In contrast, the density-dependence in the larval stages of Atlantic mackerel is extremely strong (Lett *et al*, MS 1975b) suggesting a basic difference in the recruitment mechanisms of the two species. Possibly this is related to mackerel being pelagic feeders able to prey on their own larvae, while cod are semi-pelagic or demersal, not able to feed on juveniles until they become demersal. In addition, mackerel larvae are cannibalistic, the larger larvae feeding on the smaller ones (Arnold, 1970), while the death of cod larvae is a function of the competition and starvation sequence (Ware, 1975b).

The effect of temperature on cod larvae is greater than pure density-dependence in determining the final number at metamorphosis, and this effect increases exponentially (Fig. 2A) (Bannister *et al*, 1974). Temperature acts both directly through bioenergetic responses and indirectly by controlling the food supply. Changes in temperature have been shown to be important in determining variations in primary production in the Gulf (Steven, 1974; Denman and Platt, 1975). Hjort (1914) and Jones (1973) postulate that mortality of larvae from starvation due to an insufficient supply of plankton of suitable size is the most important cause of a decline in abundance of a year-class. It follows that temperature, mediated through the density-dependent process, also could lead to a substantial mortality. However, Grauman (1973) found that the variations in food supply explained only 25% of the variations in larval abundance in the Baltic Sea. A similar study by Corlett (1965) showed that the variations in abundance of plankton explained 57.4% of the changes in year-class strength of cod stock in the western Baltic Sea. The

logarithmic nature of the relation indicated that increasing plankton densities have proportionally less effect on year-class strength. It would seem that, when temperature is below that required to produce a threshold density (Kerr, 1971) of plankton for larvae, small changes would be important in determining survival. However, when plankton reaches densities at which larvae can satiate, further rises in temperature and the resulting increases in available food would be of little importance.

Temperature affects the development rate of larvae and the time drift feeding on slow moving plankton (Sysoeva and Degtereva, 1965). Since fish living at lower temperatures have evolved to spawn larger eggs (Ware, 1975b) with larger yolk sacs associated with the larvae (Blaxter and Hempel, 1963), to survive this period, it would tend to suggest that this is an important period in the early life history of the fish. Larvae at this stage are inefficient swimmers and are extremely susceptible to predation, as well as being reliant on temperature to determine their food supply. As they grow in length, their ability to swim improves (Ryland, 1963), so that they are better able to avoid predators and gather food. Grauman (1973) can attribute 91% of the variations in cod larvae length to variations in their food supply. A rise in temperature is known to increase the appetite of fish (Brett, 1971), and the basal metabolic rate (Saunders, 1963; Beamish, 1964; Beamish and Mockery, 1964; Brett, 1964), as well as the swimming speed at which fish can search for food (Rao, 1968; Brett, 1971). Using a system simulation, P.F. Lett and F.W.H. Beamish (unpublished data) have shown the effect of temperature on appetite as one of the more important factors governing seasonal growth rates of fish.

The final density-dependent relationship and probably the most important step in the recruitment mechanism existing between larval abundance and juveniles 2 years later (Fig. 3), does not begin until the cod fry become semi-pelagic or demersal, since density dependence in the larval stage is weak. There is some evidence that cod fry remain pelagic until they are age 1+ (R.G. Halliday, personal communication). The results of juvenile surveys indicate the number of age 1+ cod associated in catches with ages 2+ and 3+ is low (A.C. Kohler, unpublished data). In accord, Ponomarenko (1973) established that the year-class strength of cod is not determined in the first year of life.

The simulated biomass was found to be sensitive to the size of cod juveniles at the end of their second year of life. This parameter was held constant at 0.30 kg, which was a long term average value. However, it was quite clear that maintaining a uniform size for cod upon entry into their demersal phase could be an important population stabilizing mechanism. The full explanation of this mechanism is dependent on the back calculation of cod growth which to date is not complete.

The l_1 size is an important link in the recruitment mechanism of the California sardine (Iles, 1973) (Fig. 9). This same mechanism can be demonstrated for Gulf of St. Lawrence herring which show a clear relationship between year-class size and l_1 length (P.F. Lett and A.C. Kohler, unpublished data). However, as previously stated, no density-dependent growth process has been demonstrated following the first year of life; therefore, the regulation of stock biomass must take place within the first year.

A constant annual growth rate will occur for age 1+ fish if the environment is stable (i.e. temperature and juvenile mackerel abundance). When maturity is a constant function of length, the size of the fish at the end of its first year of life would determine when it would mature (Burd and Cushing, 1962); thus the amount of gonadal product elaborated by the parent stock would depend only on the number of mature individuals. In this way, a wave of large year-classes would produce a wave of small year-classes much in the way described by Jones and Hall (1974). However, the smallest perturbation would cause this system to become unstable. Therefore, for a fish species which only experiences density-dependent growth in the first year of life, there must be an alternative stabilizing mechanism.

This mechanism is more clearly elucidated by considering Fig. 9. The mean abundance of l_1 sardines falls directly below the peak of the annual production curve, not the biomass curve as postulated by Iles (1973). If pelagic fish such as herring and sardines are indeed maximizing their production in the first year of life, it would imply a mechanism whereby the year-class could simultaneously tend toward a constant mean l_1 , as well as constant numbers, thereby offsetting the destabilizing forces of a random environment. The method by which both sardines and herring do this is a density-dependent process of starvation and compensatory predation, such that growth rate and mortality are inversely related (Cushing, 1975b; Ware, 1975b). There are two components to the control mechanism: accelerated growth which leads to starvation and weakening when the carrying capacity is exceeded, and, indirectly, subsequent mortality as a result of predation. Thus, efficient predators will allow the feedback time in the system to be small enough so that a sufficient number of iterations (i.e. starvation-predation sequences) can occur

for the system to reach some stable point where the production, $P = N\Delta W$, is maximized.

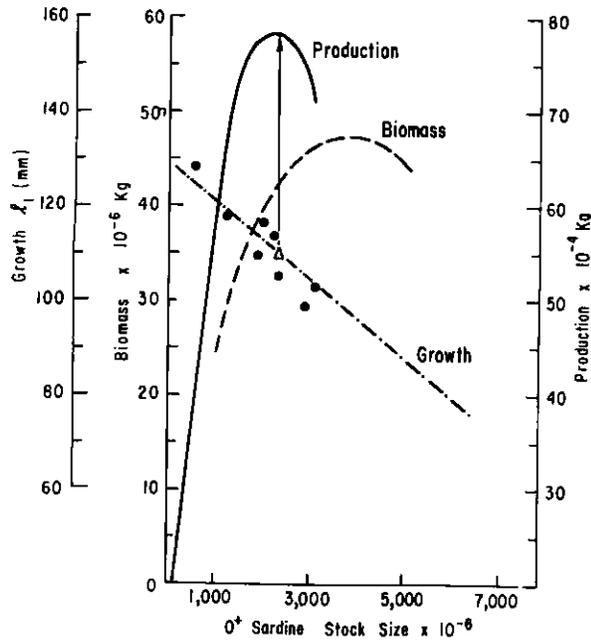


Fig. 9. Relationship between year-class size growth (l_1), biomass and annual production (Iles, 1973). The circles (o) represent the l_1 length for given year-class sizes. The triangles (Δ) represent the mean of these points which fall directly under the maximization of production. At this point the instantaneous growth equals the instantaneous mortality.

Differentiating this expression gives

$$dP = dN \cdot \Delta W + d(\Delta W) \cdot N. \quad (16)$$

If production is to be maximized, then $dP = 0$, and thus

$$dN \cdot \Delta W = -d(\Delta W \cdot N). \quad (17)$$

Rearranging the terms results in

$$\frac{dN}{N} = \frac{-d(\Delta W)}{\Delta W} \quad (18)$$

or that mortality rate is equal to the instantaneous acceleration of growth. As previously stated, accelerated growth leads to starvation. It follows that, when starvation and predation are finely synchronized, production should be maximized. For example, production was not maximized for the large 1959 year-class in the Gulf of St. Lawrence when predation was low on herring larvae immediately following the epizootic disease. In addition, the juvenile herring had a much smaller l_1 length.

Ware (1957a) has shown that pelagic fish will optimize their swimming speed to maximize their growth rate in response to a constant food concentration. Since particle concentration remains relatively constant over a wide range of particle sizes (Kerr, 1974; Sheldon *et al*, 1972, 1973), it follows that growth rate of pelagic fish is a response to the turnover rate (P/B) of their food supply. Turnover rate is a power function of body weight (Kerr, 1974); thus the ecological efficiency is merely a reflection of the ratio of the weights between predator and prey when production is maximized. Since swimming speed is closely related to length, it follows that pelagic fish would evolve such that

their length was related to the particle size of food on which they were feeding, and that the variance in their length would reflect the range of particle sizes available to them as forage.

This mechanism may only be true for fish stocks which exhibit no cannibalism at the juvenile stage, but only competition. The major predator of 0+, 1+, and 2+ cod is usually older cod (Bigelow and Schroeder, 1953; Ponomarenko, 1965), presumably a major population control factor. Ponomarenko (1973) established that older cod usually do not feed on juveniles after they reach 10 cm in length; however, Bigelow and Schroeder (1953) state that adult cod feed on their juveniles until they are over 20 cm in length. Therefore, an alternative density-dependent mechanism must be operating, and this mechanism gains in importance as the cod grow. The 1+ and 2+ cod at high densities could overcrop the available food supply. In the Gulf, small cod (11-20 cm) feed primarily on a limited number of food forms consisting of mysids, euphausiids and amphipods (Powles, 1958). The turnover time required for the populations of these organisms to build up again after depletion would be relatively long. Thus, overcropping could lead to a reduction in nutritional status of young cod, again making them more susceptible to predation (Ponomarenko, 1961).

The entire cod production system is constrained by the pelagic fish biomass, and the model of this paper represents the fishery when it is operating within the constraint of constant total pelagic biomass. During 1955-59, year-class strengths of cod were well correlated with a severely reduced total pelagic biomass brought about by the epizootic disease in the Gulf of St. Lawrence (Sinderman, 1958). At that time, year-class strengths were excessive with the 1956 year-class being twice as large as any observed before or after this epidemic. This is explained by the carrying capacity for young cod being substantially improved, since the energy harvested by pelagic fish species could now be transferred into food organisms eaten by juvenile cod. The growth rate of adult cod also improved (Kohler, 1964) due to increased availability of food, which may have substantially incremented the production of eggs for a given population number. The homeostatic mechanisms regulating the abundance of cod must fit within the carrying capacity left vacant by pelagic species. As the population is being reduced by exploitation, the surplus energy is simultaneously being synthesized into both somatic and gonad growth. Thus, the attainment of maximum growth rate is the lowest level of population biomass at which the stock can replace itself on an annual basis.

SIMULATION RESULTS

Three types of management strategy were considered: fixed catch quota, fixed fishing mortality (effort quota), and maintenance of a fixed spawning stock biomass.

In the absence of fishing, the simulated stock size exhibited a cyclic behaviour, rising from 50,000-60,000 tons to 250,000-300,000 tons in 6-8 years, declining slowly for 6-8 years and declining sharply to 50,000-60,000 tons in 6 years. About 15 years were required for one cycle.

The introduction of a catch quota of 10,000-15,000 tons in the winter fishery reduced the peak biomass, but the cyclic behaviour was qualitatively unchanged. The associated levels of fishing mortality varied from 0.04 to 0.4. Increasing the quota to 20,000-25,000 tons did not remove the 16-year cycles in biomass and effort. When the quota was raised to approximately 35,000 tons, the stock declined to zero after five cycles. Changes in the quota level had little effect on the amplitude of the natural cyclic trend (Fig. 10) in biomass and led to high levels of fishing mortality at low population biomasses.

The effects of equal, constant fishing mortality rates for the summer and winter fisheries is illustrated in Fig. 11. Simulations were run for 50-100 years to ensure that the effects of the initial conditions were removed. Mean catches and standard deviations were calculated from a 10-year series after simulation had stabilized. A fishing mortality rate of $F = 0.2$ resulted in irregular fluctuations in biomass between 100,000-200,000 tons with catches averaging 31,000 tons with a standard deviation (SD) of 2,900 tons. Increasing F to 0.4 reduced the range of fluctuations to 65,000-175,000 tons with mean catch of 42,000 tons and SD of 2,200 tons. When F was 0.7, the spawning stock biomass stabilized at 85,000 tons with a catch of 53,000 tons and SD of 250 tons. Increasing F to 0.9 caused the stock biomass to become unstable and decline to zero. Fig. 13A shows the relationship between fishing effort and yield and Fig. 14 shows the relationship between fishing effort and SD of catch. The scatter of points in Fig. 13A is due to the inclusion of simulations with unequal allocation of effort to the two fisheries.

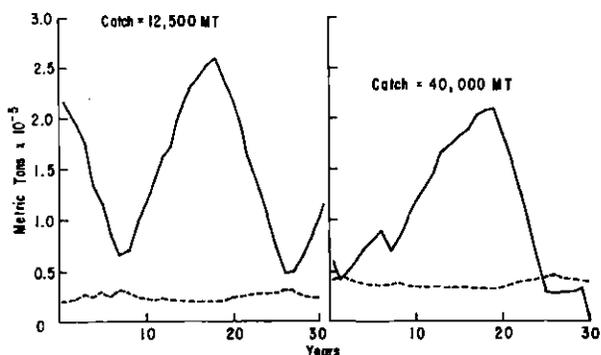


Fig. 10. Fluctuations of biomass and catch under two levels of catch quota control. (Biomass = solid line; winter fishery catch = dashed line.)

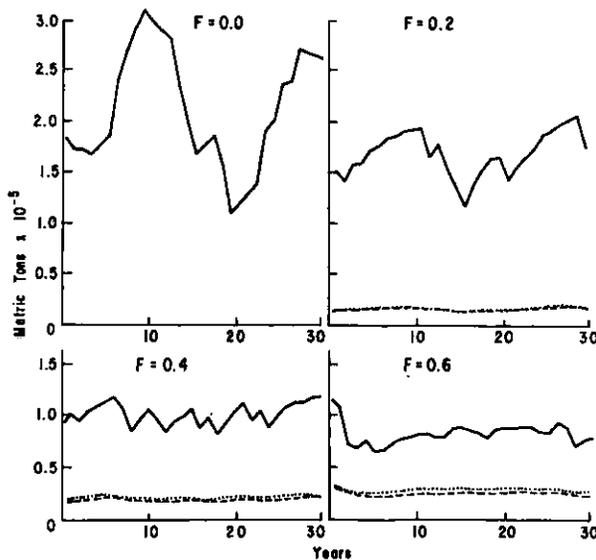


Fig. 11. Fluctuations of biomass and catch under four levels of constant fishing mortality rate, equally divided between summer and winter fishing. (Biomass = solid line; summer fishery catch = dotted line; winter fishery catch = dashed line.)

In order to study the effects of differing allocations of effort to the two fisheries, simulations were carried out with the total fishing mortality rate in the range of 0.3-0.6. The results are given below:

F (Summer)	F (Winter)	Total yield (000 tons)
0.10	0.20	37.1
0.20	0.10	42.4
0.15	0.30	40.9
0.30	0.15	47.6
0.25	0.25	48.2
0.20	0.40	50.3
0.30	0.30	49.8
0.40	0.20	51.8

In all cases, the yield was increased by allocating more fishing effort to the summer fishery than to the winter fishery.

The results of simulations involving biomass control are illustrated in Fig. 12 and 13. In these simulations, the summer fishing mortality rate was zero. The results are as follows:

Biomass (B_{SS}) $\times 10^{-3}$ (tons)	50.0	92.0	120.0	150.0	170.0
Yield $\times 10^{-3}$ (tons)	52.0	52.5	42.7	44.3	31.5
SD of yield $\times 10^{-3}$ (tons)	13.0	3.8	19.7	2.3	13.4

Recruitment fluctuations were smallest near 90,000 and 150,000 tons.

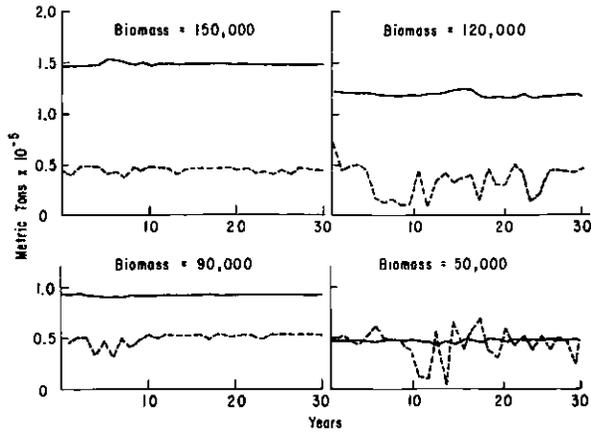


Fig. 12. Fluctuations of biomass and catch under four levels of biomass control. (Biomass = solid line; winter fishery catch = dashed line.)

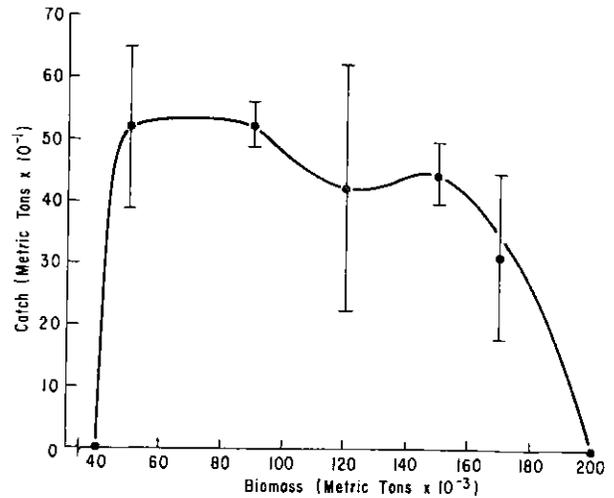


Fig. 13. Relationship between controlled level of biomass and average yield. The bars represent one standard deviation in annual catch.

MODEL LIMITATIONS

In the study of a natural system as large as the cod stock of the southern Gulf of St. Lawrence, it is not possible to take observations of stock size, temperature and other variables at all of the levels necessary to accurately define response surfaces over the whole range of stock sizes and environmental variation. One cannot recommend overfishing a stock in order to study its behaviour on the verge of collapse. While accepting this constraint and attempting to make the best use of the available data, the analyst should note the areas where response surfaces are poorly supported by the available data. With the exception of the 1973 value of 63,000 tons in the egg production analysis, the stock biomasses used in the derivation of the model equations lay in the interval 120,000-240,000 tons. The model equations predict egg productions which approach zero and subsequent minimal recruitments for biomasses below 40,000 tons and above 200,000 tons. While these predictions are qualitatively reasonable since, for example, there can be no egg production at zero biomass, the accuracy of quantitative predictions diminishes sharply with increased deviations from the mean of the observed biomasses.

Although, under favourable environmental conditions, numbers of larvae in excess of $10^5/1,000 \text{ m}^3$ are predicted, the maximum larval abundance used in fitting the equation predicting age 2+ recruits was $2.5 \times 10^4/1,000 \text{ m}^3$, so that predicted low recruitments due to excessive egg and larval numbers at stock biomasses near 125,000 tons are unsupported by observation. The transformation of egg production is deemed responsible for this artificiality.

The implications of these limitations on the behaviour of the model are that recruitment predictions at very high and very low levels of stock biomass are quantitatively unreliable, although qualitatively acceptable, and that the predicted variability of recruitment at biomasses near 125,000 tons may be exaggerated. Thus, the quantitative simulation results for strategies involving excursions into regions of very high and very low biomass are not well supported. Fortunately, strategies involving such extreme biomasses are less promising than those with biomass variations between 90,000 and 190,000 tons, so that the practical management of the fishery is not affected. The asymptotic nature of the equation predicting age 2+ recruits may result in an unrealistic stabilization of recruitment for biomasses below 100,000 tons, so that yield at high levels of fishing mortality may be overestimated. The predicted fluctuations in recruitment near 125,000 tons have some influence in depressing yield and substantial influence in increasing the variability of catch from year to year (Fig. 13).

A weight of 0.3 kg was assumed for age 2+ fish independently of events in the fishery. It is likely that this weight, in fact, varies with year-class size and stock biomass, although no substantial evidence supporting this hypothesis is currently available. A possible biological mechanism whereby fish tend to stabilize l_1 and l_2 length is

discussed in the following section. Quantitative results of simulations are sensitive to the weight of age 2+ fish with higher yields and excursions into regions of higher stock biomass when this weight is increased, although qualitative results are similar.

The model equations were derived with observations during a period when the pelagic (herring and mackerel) fish biomass was fairly constant. There is evidence that environmental carrying capacity for cod is inversely related to the pelagic fish biomass. If the herring and mackerel stocks in the Gulf of St. Lawrence were depleted, as happened in 1959 with an epidemic of the epizootic disease, cod growth rates would increase (Kohler, 1964) and maximum egg production for cod would occur at a higher stock biomass. Thus, the simulation results are conditional on stability of the pelagic biomass.

DISCUSSION

Three methods of regulating the fishery have been considered: (i) catch quota, (ii) effort, and (iii) biomass control. The strategy of constant catch quota does little to damp the 15-year cycle of the unfished stock (Fig. 11). The upshot of this strategy is large fluctuations in fishing mortality rates, these rates increasing as the stock declines. In essence, the control of catch tends to augment the natural cyclical nature of the fishery and leads to stock collapses at levels below what is considered to be the maximum sustainable yield (MSY). Depending on the management strategy the MSY is between 40,000-50,000 tons. However, with an annual catch quota of only 35,000 tons, the stock eventually collapses. While the length and amplitude of the simulated cycles depends on the age at first maturity and the population structure, the amplitude of the simulated fluctuations may differ somewhat from those of the actual stock. The maximum catch which can be taken each year is not well defined, but it is clear that quota management is the poorest of all three choices since it does nothing to stabilize the stock biomass at a productive level.

A steady increase in yield with a reduction in variance results from the control of fishing mortality (analogous to effort control) (Fig. 12). The natural cycles of the unfished stock are opposed by taking larger catches above the average biomass and smaller catches below it. Simulation studies indicate a stabilization of biomass at 85,000 tons and a catch at 53,000 tons, when $F = 0.6$. When F increases to 0.9, recruitment becomes unstable and the stock eventually crashes (Fig. 14). The stability in the stock is a result of the relationship between larvae and the abundance of age 2+ recruits (Fig. 3). When the stock biomass is low the curve becomes flat-topped, so that wide variations in larval number due to environmental influences and near maximum egg production result in very little change in the recruitable year-class size. However, when the stock is maintained below 100,000 tons, the fishery is on the edge of the precipice (Fig. 14A) and relies on a succession of maximal recruitments. In view of the lack of supporting biomass observations below 100,000 tons, the precise location of this precipice cannot be determined from the current model, and to adopt a level of $F = 0.6$ risks a collapse of the fishery.

Simulation results indicate that more effort should be applied to the summer fishery than to the winter fishery. This strategy improves the average level of recruitment for a given total F by reducing B_{SS} and also has the benefit of allowing the winter fishery to be used to "trim" the parent stock biomass on the basis of results from the summer fishery. Since the fish are much more highly concentrated in the winter fishery, they are much more accessible to trawling. Over the years, this has resulted in the stock being "fished-up" to the point that only one year-class is primarily responsible for production of eggs. These mainly age 4+ and some age 3+ cod are going to spawn for the first time in the following spring and must be allowed to do so in order to maintain the stock. Therefore, when stock biomass is low, comprised of mainly young fish, the fishery should be maintained at an extremely low level.

The strategy of controlling spawning stock biomass enables larger catches to be taken at lower levels of F than is possible by effort control, although fluctuations in fishing mortality require the effort levels to fluctuate. Fluctuations in catch are comparable at low levels of F , with somewhat smaller fluctuations using biomass control. Managing the stock biomass at 90,000 tons gives a slightly higher yield and variance in yield than setting F at 0.6. Because of the nearby constant recruitment at this stock size, the two strategies are almost equivalent. Regulating biomass is possible at 50,000 tons at the cost of large fluctuations in catch and effort; this is not possible with a fixed effort quota. The striking decline in yield and increase in variance resulting from fixing the biomass at 120,000 tons (Fig. 13) is a result of being on the peak of the egg production curve. Large numbers of larvae are being produced at this level of egg production. Due to the effect of biomass in reducing the number of recruits when larvae are abundant, the

result is considerable fluctuations in recruitment and hence in catch with a slight loss in yield. The extreme stability of catch at 150,000 tons is due in part to the location of the biomass half way down the right limb of the egg production curve which would assure stable recruitment (Fig. 2). In addition, biomass is located near the point of inflection of the growth rate relationship, so that small deviations in biomass are quickly compensated for by instantaneous changes in growth, thus maintaining biomass naturally at a constant level. As well as being able to respond to fluctuations in fishing intensity within a year, it can also equilibrate quickly to fluctuations in recruitment.

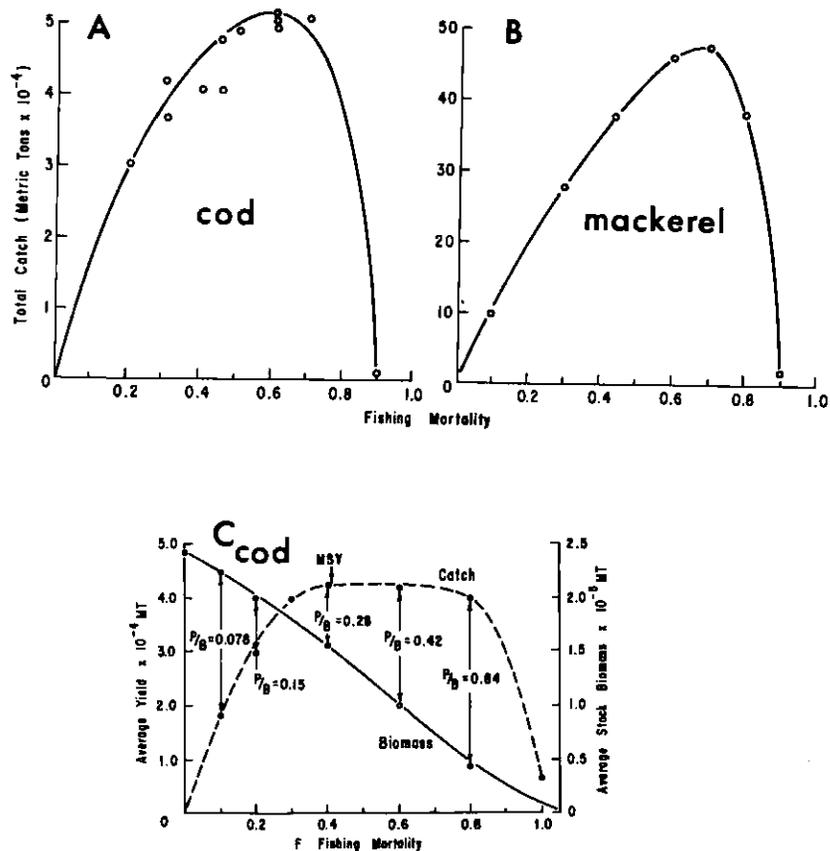


Fig. 14. Relationship between fishing mortality and catch when the environment is random (A) and fixed (B). When the environment is stable, recruitment at levels of F over 0.4 are nearly constant, thus sustaining a high level of catch (C). The precipitous side of the curves are brought about by a recruitment failure.

The importance of random fluctuations in determining the relation of yield to fishing mortality is evident in the comparison of Fig. 14A, B, and C. Fluctuations in recruitment reduce the yield at low levels of F, shortening the plateau near constant yield in Fig. 14C. The comparison of the yield vs fishing mortality curves for cod and mackerel (Fig. 14B) indicates a similar relationship between the two species, with the production of mackerel being 10 times greater. This observation is not without ecological significance since mackerel occupy a trophic status one level below cod. The variance in catch was found to change considerably with changes in the levels of fishing mortality or biomass control (Fig. 15). The failure of management by constant catch quotas was mainly due to cyclic trends in stock size and recruitment, although random variation in recruitment was responsible for the collapse of the fishery at high quota levels.

The two components of variation in recruitment, consisting of cyclic trends induced by the lag time between egg production and recruitment and random, environmentally induced, fluctuations in recruitment, are the causes of the differing behaviour of the simulations

under different management policies with the same average yield. In order to obtain consistently high catches with a resulting high average catch or yield, it is essential to stabilize the stock biomass in a productive region. In this model there are two stable productive regions, one near 90,000 tons when stability arises through constant recruitment, and the other near 150,000 tons where stability is partly due to consistently high recruitment and partly due to adjustments in the growth rate to changes in stock biomass. The higher catches at 90,000 tons are due to the capture of 3-year-olds, which is potentially dangerous, if cod maturity is a function of length as well as age (Daan, 1974). Also, some of the improved catch can be attributed to an increase in growth rate. The behaviour of the model in the neighbourhood of 150,000 tons has a sounder biological basis than that near 90,000 tons. These two regions are represented by the mid-points of the ascending and descending limbs of the egg production curve; however, 150,000 tons also represents the point of greatest elasticity of growth rate.

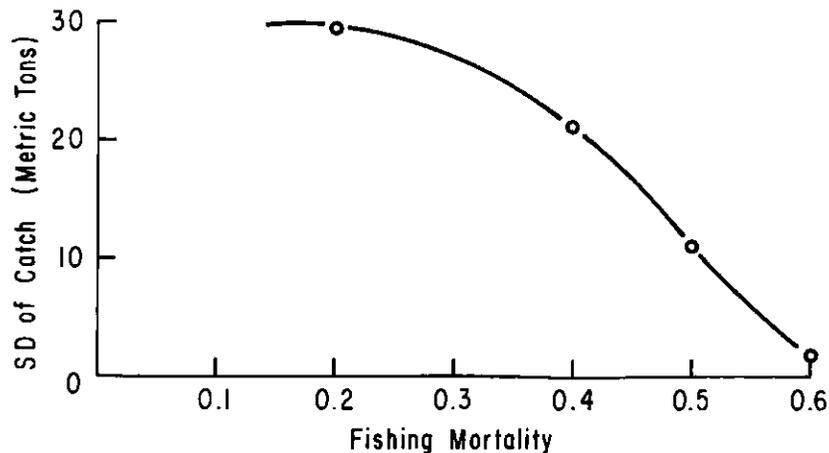


Fig. 15. Relationship between controlled level of F and SD (standard deviation) of catch.

Relation to production models

The behaviour of the system model under management strategies of constant effort quotas or biomass regulation may be compared with that of general production models (Schaefer, 1954, 1957; Pella and Tomlinson, 1969; Fox, 1970). Schaefer derived a continuous time model for the dynamics of a fish stock biomass under the assumption of instantaneous response of rate of change of biomass to changes in population density independent of the age composition of the stock. His basic equation is

$$\frac{dB}{dt} = Bf(b) - qXB \quad (19)$$

where $f(b)$ is a linear function of biomass B , X represents fishing effort and q the catchability coefficient. Pella and Tomlinson (1969) generalized this equation by setting

$$f(B) = HB^m - KB \quad (20)$$

where H , K and m are constants. Fox (1970) modified Schaefer's model to incorporate a Gompertz growth curve

$$f(B) = K(\ln B_\infty - \ln B). \quad (21)$$

Schaefer's model implies a quadratic relation between fishing effort and yield while the extension of Pella and Tomlinson allows this curve to be skewed. Fox's model implies a highly skewed relation between equilibrium yield and fishing effort rising, steeply from zero at no effort to a maximum corresponding to a stock size approximately 33% of the maximum and declining slowly with increased fishing effort.

While the relationship between biomass and yield derived from the simulation model (Fig. 13 and 14) resembles those of Pella and Tomlinson and Fox, the relationship between

yield and fishing mortality may be described as one half of Schaefer yield curve, with yield rising quadratically as F is increased from 0.0 to 0.6 and dropping discontinuously to zero at some point between $F = 0.6$ and 0.9.

While the growth rate of fish can respond instantaneously to changes in stock biomass, the recruitment mechanism requires years to compensate to such changes. Thus, an unfished cod stock exhibits cyclic fluctuations which do not arise in the continuous time production models. Agreement with the production models is good in the region of stock biomass between 150,000 and 200,000 tons, where density-dependent growth is a regulating factor. At low levels of biomass, they differ due to complete reliance on recruitment to compensate for biomass fluctuations.

Continuous time models involving structure fluctuations have been studied (Kendall, 1949; May, 1974), but the fluctuations were infinitesimal and have quite different implications from those of variation in recruitment which are macroscopic. The absence of such large scale disturbing factors led Fox to conclude that "it is not necessary to place such a tight restriction on the level of fishing mortality as implied by the linear model to maintain an equilibrium yield close to maximum", and, although he noted that "beyond the region of maximum equilibrium yield, the reduced population is generally thought to become 'sensitized' to adverse environmental conditions", he nevertheless advocated the use of a catch quota system as making the choice between his model and Scahefer's unnecessary. Due to the time lag of the recruitment mechanism of cod, the attempt to regulate the fishery by annually removing the maximum yield leads to extreme instability and rapid collapse of the stock. Pella and Tomlinson suggest that the size of the stock be maintained at some intermediate, most productive, level between the maximum population size and extinction through catch or effort restrictions. This conclusion is more circumspect and is in agreement with the simulation results, provided a constant catch quota is not adopted.

It is common practice to estimate the parameters of a production model from catch and fishing effort data. In the model of this paper, this method would be satisfactory if effort were held constant for twenty years at each of a series of levels. Unfortunately, observations of catch and effort from a fishery usually form a time series and often involve a trend in effort over the data series. The application of this method of estimation to the simulation model would lead to unpredictable results due to the response time of recruitment. At low levels of F , the cyclic trend of biomass would be more influential than the level of fishing effort for a short time series. If F were steadily increased from a low level, the relation of catch to effort would be dominated for at least ten years by the initial state of the stock. The use of moving averages of effort would also be unreliable. Thus the "1/2 Schaefer curve" of Fig. 14 might not arise from an analysis of a catch and effort series of, for example, twenty years. Although a general production curve relating yield to fishing effort emerges from the structure of the simulation model, fitting such a curve from catch and effort data is not advisable.

If reliable information on age composition and weight at age is available for commercial catches, it may be possible to estimate the age composition, and hence the stock biomass, over the history of the fishery using virtual population analysis (Murphy, 1965). If a relationship could be found between stock biomass and recruitment, and if the response of growth rate to stock biomass were known, then a production curve might be fitted using these relations. It would be wise, however, to manage the fishery at some level of biomass above that promising the maximum yield, at least until the effects of recruitment fluctuations were determined.

Simulation results indicate that management of the cod stock biomass at the point of inflection of the relationship between growth and biomass results in high yield with stable catches. Managing a stock exhibiting density-dependent growth at this point of inflection has a sound biological basis. It is at this point that the stock is best able to compensate environmental fluctuations with changes in somatic and gonad growth, responding to small perturbations directly, as in the general production models, and to larger perturbation by changes in egg production and, hence, recruitment. The gain in yield offered by maintaining the stock biomass at a level maximizing the growth rate is obtained at the expense of an impaired ability to respond to the further stress of unfavourable environmental conditions.

Simulations indicate that the cod stock is unable to maintain a production to biomass (P/B) ratio above 0.8 but it is able to sustain a P/B ratio of 0.6 indefinitely. This result suggests that in the absence of more detailed data, it is wise to manage a fish stock at a level below that giving an estimated maximum P/B ratio and the value of 0.6 may be a useful rule of thumb.

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