THE BIOLOGY AND FISHERY OF AMERICAN PLAICE (HIPPOGLOSSOIDES PLATESSOIDES(FABRICIUS)) WITH SPECIAL REFERENCE TO THE GRAND BANK

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The Biology and Fishery of American Plaice (*Hippoglossoides platessoides* [Fabricius]) with special reference to the Grand Bank

by

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ABSTRACT

American plaice (Hippoglossoides platessoides) is widely distributed throughout the Northwest Atlantic with the Grand Bank supporting the largest population. Meristics indicated possibly considerable intermingling during pre-metamorphosis stages, but on the Grand Bank at least tagging and growth data suggested little intermingling beyond the early life history stages.

Length-age comparisons indicated considerable differences between localities and also gave positive correlations between average length at ages 5 and 15 and probable bottom temperature.

Peak spawning occurred from early April on Flemish Cap to early June off Northeast Newfoundland and Labrador. Fifty percent (50%) sexual maturity for different localities occurred at 7.8-12.2 years for females and 5.3-7.5 years for males.

Log-log relationships were established between fecundity and fish length, gutted and gilled weight, and age for Grand Bank samples. No differences were found between fecundity-length relationships for different parts of the Grand Bank.

Although invertebrates, principally benthic forms, occurred most frequently in plaice stomachs from the Grand Bank, capelin and lance made up a major part of the total

food weight and were especially important for the southern Grand Bank.

Landings of Grand Bank plaice increased from the early 1950's and reached a peak in 1966-68 with a subsequent gradual decline. Increased exploitation was reflected in declines in catch per hour, stock abundance and fishing mortality rates. Stock assessments suggested that removals in the immediate future may be lower than in previous years. However, because of non-reporting of discards of plaice, prediction of yield is difficult.

Average length at age increased from the early 1950's to the 1970's apparently because of increased rate of growth in the early years of life and coupled with this was a decline in age at sexual maturity. Significant correlations were found between stock size, asymptotic length (L_∞) and size at age 5 and 10 years for the northern half of the Grand Bank.

Acknowledgements

I wish to acknowledge the assistance and advise given by a number of people in doing the research and preparing the results for this presentation. I am especially grateful to Dr. W. Templeman former Director of the Newfoundland Biological Station who provided guidance and advise especially in the early parts of the research program. Additionally various members of the scientific staff of the Biological Station gave advise and suggestions in the analysis of the data and in particular I wish to acknowledge the help of Mr. A.T. Pinhorn and Mr. R. Wells. I also wish to acknowledge the help given by Dr. J.M. Green and Members of my Committee in the preparation of this thesis.

Various members of the technical staff contributed greatly to the research program in the collection and pleminary preparation of data. In this respect I am particularly indebted to Messrs. C.A. Rose and C. Butt for most of the work involved in age determination and various compilations. Finally I wish to thank Mrs. H. Luffman and Miss Cathy Pitt for the arduous task of typing this manuscript.

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GENERAL INTRODUCTION

In the past decade American plaice (Hippoglossoides platessoides [Fabricius]) has become one of the major commercially exploited groundfish species in the Northwest Atlantic. For the Canadian fishery on the Grand Bank (International Commission for the Northwest Atlantic Fisheries [ICNAF] Divisions 3L, N and O) especially for Newfoundland-based trawlers, it is of particular importance accounting for approximately two-thirds of total landings.

Deep sea otter trawlers were first used by the Newfoundland fishery on the Grand Bank during late 1940's and early 1950's. Up to the mid-1960's most of the fishing effort was directed into catching haddock. However, with the drastic decline in this species, the expanding Newfoundland fleet diverted a large proportion of its total effort to catching American plaice and since that time, it has become one of the mainstays of the offshore fishery. At the same time a considerable amount of effort by some of the Eastern European countries, principally the USSR produced considerable landings of plaice.

This thesis presents a study of the various phases of the life history and population dynamics of this species. This information was used to provide biological information for the rational management of American plaice on the Grand Bank. A major proportion of the research has been directed at

Grand Bank American plaice.

Included in the plan of research were studies on stock delineation using meristics and tagging to determine whether discrete stocks could be separated, studies on maturity, fecundity, age and growth, and food and feeding. An assessment of Grand Bank American plaice is presented and from this type of presentation and annual updating recommended levels of removals are determined. It is felt that a thorough knowledge of all phases of the biology of a species is required before one attempts to apply models aimed at stock regulation.

In presenting the results of this research, it was felt that the most logical form was a presentation in three sections. Thus, Section 1 contains the investigations into the life history or general biology. Section 2 is a presentation of a stock assessment and is intended to shed light on the present management scheme and also reveal some of the difficulties involved in applying a modified "Virtual population" (Pope's Cohort analysis) model to this stock. Section 3 relates changes in fish length at comparable ages and a decrease in size at sexual maturity to an apparent reduction in stock abundance because of increases in levels of exploitation.

Finally some general conclusions are presented that hopefully places the Sections in perspective in relation to the total problem of stock management or in other words focuses on the prime objective of arriving at a proper management technique by applying all available knowledge of the particular stock.

SECTION 1 THE BIOLOGY OF AMERICAN PLAICE

Introduction

In this section information on the biology of Hippoglossoides platessoides will be presented and discussed. Some of this information has been presented in an expanded form in previous publications by the author, and here it is summarized and intergrated with more information to give a general overview of this species.

Besides published work by the author (see References) Frost (1938) presented data on egg and larval distribution of plaice and some general biological observations (1940). Yanulov (1962) gave some information on age and growth of plaice in this area and Nevinsky and Serebryakov (1973) information on plaice spawning. Minet (1972) reported on length and sexual maturity and food and feeding (Minet 1973) of St. Pierre Bank plaice.

Material and Methods

Distribution in the Newfoundland area of the Northwest Atlantic

The information on distribution of plaice came entirely from research sets by the A.T. Cameron from 1958-73. Only successful sets with the 41-5 otter trawl (modified standard Commercial net) using a cod end liner of ½ to 1½ inch (127-281 mm) nylon netting were tabulated. The objectives of the research cruises were many and varied. Most of the sets were made on predetermined transects across the slope of the shelf with sets occurring at a number of regular depth intervals. All sets in the units were used to calculate average numbers in (Fig. 3-6) units 1 degree longitude by 30 min. latitude.

Up to 1971 groundfish surveys of the Grand Bank and St. Pierre Bank were also carried out on the transects system, but in 1971 a stratified-random method of survey was initiated. With this method the two banks were divided into a number of strata which were again divided into a number of small unit areas (Grosslein and Pinhorn 1971). Fishing locations were selected at random from these small units.

Distribution in relation to temperature and depth

To show the relationship of distribution to temperature and depth only data from Divisions 3L and 3N were tabulated (Fig. 7) since information from other localities produced too few observations at various temperature-depth categories.

A cruise during the fall of 1968 was designed to indicate distribution of plaice within a 30 sq mile area on the eastern slope of the bank (Fig. 8). For these data, weight of fish caught at the various depth and temperatures were recorded for each set.

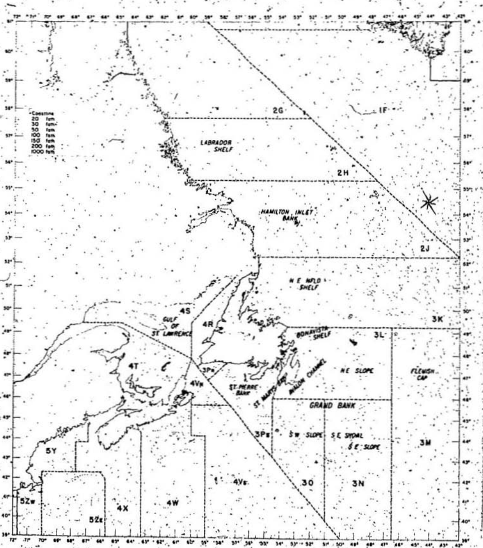

Fig. 1. Map of the Northwest Atlantic showing ICNAF Divisions and places mentioned in the text.

Vertebral and anal fin ray counts

All whole vertebrae between, but not including the basioccipital and hypural bones were counted. An average of about 2% had fused vertebrae and were discarded (Pitt 1963). Flesh was removed from the columns by cooking and then spraying with water from a rubber hose. Anal fin rays were counted either on preserved or fresh specimens using a candling table. Care was used to determine that split rays were counted as coming from a single base. For both vertebrae and fin ray studies random samples were taken from research vessel catches during normal research cruise operations.

Tagging

There were five main tagging experiments and these are listed in Table 1 and the locations indicated on Fig. 2. Petersen disc tags were used for all experiments. These were about 0.5 inches (13 mm) in diameter, 0.036 inches thick (0.91 mm). Tags were attached by 0.032 inch (0.8mm) nickel wire. Details of tagging procedures are given in Pitt (1969). Generally only fish commercial size or over 26-28 cm were tagged.

Nearly all recoveries were from commercial otter trawlers. Some returns were from deck hands who had little knowledge of the vessel's fishing locality, also some tags were

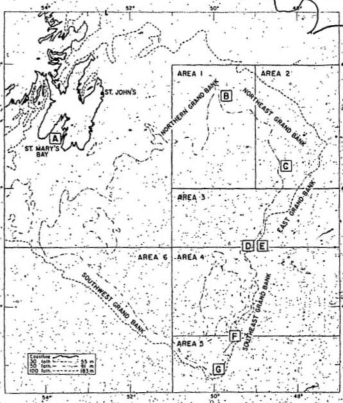

Fig. 2. Map indicating tagging localities as listed in table 1 (page 9) and the areas that were used in interpreting the returns.

Table 1. Information on tagging localities, and numbers tagged with various combinations of upper and lower discs of the Petersen tags. (Letter refer to location in Fig. 2).

Locality	Date	Tagging Depth fath	Tagging Depth m	Orange / Orange	Yellow / Yellow	Yellow / White	White / Yellow	White / White	Total Tagged
(A) St. Mary's Bay	June 1954	70-86	128-167	449	-	-	-	-	499
(B) N Grand Bank	Oct. 1954	58-61	106-116	1000	-	-	-	-	1000
(C) NE Grand Bank	June 1961	40	73	-	35	40	34	36	145
" " "	" "	52	95	-	27	25	29	24	105
" " "	" "	64	117	-	248	232	211	201	892
(D) East Grand Bank	Sept. 1960	78-80	143-146	-	83	-	-	-	83
(E) " " "	June 1961	39	71	-	160	156	160	162	638
" " "	June 1961	60	110	-	90	94	70	70	324
(F) SE Grand Bank	July 1959	50	91	778	-	-	-	-	778
(G) S Grand Bank	July 1959	39	71	197	-	-	-	-	197

recovered in cutting rooms at fish plants. In both of these cases it was usually difficult to document the recovery site. In plotting locations of tag recoveries, only returns with reliable information were used.

Calculation of growth curves

As for the data on distribution growth curves were prepared from samples collected during regular survey cruises by vessels operated by the St. John's Biological Station.

A description and validation of age interpretation by otoliths is presented in Pitt (1967) with particular emphasis on research vessel samples at St. Mary's Bay, Newfoundland. In all cases, different growth curves were presented for males and females.

The most widely accepted form for expressing growth is the Von Bertalanffy equation: $l_t = L_\infty \left(1 - e^{-K(t-t_o)}\right)$ where l_t is length at age t (in years), L_∞ is the theoretical maximum length, K is a constant expressing rate of change in length increments with respect to t, and t_o is the hypothetical age at zero length. For curves comparing growth for different localities the method suggested by Ricker (1958) was used, however, for growth comparison series in Section 3 the Von Bertalanffy growth curves were fitted using a weighted least square fit (Allen 1966).

Because of probable differences in growth throughout the year, samples collected January to June only were used.

Sexual maturity and spawning

Maturity stages - Reproductive stages used in determining spawning time and age and size at sexual maturity are described by Pitt (1966). In determining stages of sexual maturity, there was always the problem of deciding if gonads were maturing for the first time or had recovered from a previous spawning. Usually this was very difficult to determine in smaller sizes of mature females after late July and early August unless residual eggs were present from previous spawning. Thus in size and age at sexual maturity calculations, only plaice taken just prior to and immediately following the spawning period were used.

Spawning time - In determining spawning time, only females were used because some of the males that were recorded as "spent" or "partly spent" may have in fact been in the "ripe" condition. Since there obviously must be males to fertilize the eggs, only females were important in determining spawning time.

Age and length at sexual maturity M_{50} - Age and length when equal numbers are immature and mature is commonly defined as the 50% maturity point or M_{50}. Bliss (1935a, b; 1952) in assessing the effects of various dosages of poisons and vitamins on animals presented a method for calculating LD_{50}, which in the case of poisons is the point at which 50% of the animals were dead. Fleming (1960) used the same method to determine age at 50% maturity of Newfoundland cod with the only difference being that in fitting the provisional line (Bliss 1952) a better fit was obtained here by using, as did Bliss, log "dosage" which in this case was percentage mature plotted against log age on probability paper.

Collecting, preserving and sampling for fecundity studies

Details of sampling time, etc., are given in the following text table. Some of the ovaries were collected and preserved at sea in which case weights of fish and gonad weights were not recorded; the remainder were collected from specimens examined in the laboratory.

Area	Date	Number
St. Mary's Bay	Feb. 26, 1957	18
St. Mary's Bay	Apr. 23, 1958	10
N. Grand Bank	Apr. 3, 1958	19
N. Grank Bank	Apr. 29, 1958	13
S. Grand Bank	Feb. 26, 1958	29
S. Grand Bank	Mar. 7, 1961	14
S. Grand Bank	Feb. 11, 1962	37
	Total:	140

Fish lengths used were total lengths to the nearest centimetre. Fish were gutted and gilled (i.e. with gills, alimentary canal and associated organs and gonads removed), and weighed to the nearest gram.

All ovaries were collected before any eggs were translucent, approximately 1 to 2 months prior to spawning. At this stage there is no possibility of counting eggs that will mature the following year since average diameter of maturing eggs of the present year is approximately 0.8 mm whereas eggs of the next generation are less than 0.3 mm.

Ovaries were placed in jars containing Gilson's fluid (as modified by Simpson (1951)) which facilitated the breaking down of ovarian tissue and were allowed to remain in this solution for periods of from 3 to 6 months. The 3-month period was found to be best for cleaning eggs since for greater periods the outer ovarian wall became soft and could not be peeled away.

In removing ovarian tissue from the eggs the following method was found to be very satisfactory. Ovaries were placed on fine bolting silk stretched over a large funnel and were broken apart so that parts of the tougher outer walls could be removed with forceps and the remainder of the cleaning was accomplished using a gentle stream of water. After connective tissue had been satisfactorily washed from the eggs the latter were put into a solution of 10% formalin and stored until counting.

Sub-sampling was accomplished by means of a whirling vessel, an apparatus originally designed by E. Lea and G. Rollefsen of the Fisheries Directorate, Bergen, Norway, as a means of sub-sampling plankton samples. Its structure and operation are described in detail by Wiborg (1951). Some modifications were made to this equipment to facilitate the sampling techniques (Pitt 1965). Details of the sub-sampling methods and tests of accuracy of the equipment are contained in Pitt (1964).

Food and feeding

About 5000 stomachs were collected from 1964 to 1971 on cruises of the research ship A.T. Cameron. For all years except 1971 sampling stations were on transects across the slope of the bank at 20 fath (37 m) depth intervals from 40 to 150-160 fath (73-290 m). Shallower than 40 fath (73 m), stations were normally placed between 10 and 15 nautical miles apart. In 1971 the fishing stations were selected randomly from strata into which the whole area was divided as previously mentioned.

Stomachs were collected from a limited number of fish from each set in 5-cm length categories. In analysing data by length, samples were combined in 10-cm groups. Stomachs were removed from fish almost immediately following capture, injected with a 5-10% solution of formalin and preserved in a similar solution for later examination. Stomach contents of each fish were separated into individual items and damp weights were determined to an accuracy of 0.01 g.

Some invertebrate organisms (particularly annelids and crustaceans) could only be classified to order or phylum, mainly because of digestive action, but this was no drawback since the primary objective was to classify contents according to major groups with classification to species being of lesser importance.

Because sampling occurred at various localities at different seasons over a number of years, the general procedure was to combine data for the areas under consideration.

A comparison of a small number of fresh and formalin-preserved sand dollars, starfish and clams gave weights varying from 97 to 103% of the fresh condition after preservation in sea water formalin for 1-2 months. Capelin preserved in 10% formalin were 97-99% of their original weight after 30 days. The weight of the formalin-preserved material was therefore treated as fresh or live weights for estimating rough caloric values of food.

Caloric values for live weights of phyla from

Brawn et al. (1968) were applied to the weights of various major food items recovered from the stomachs. Although some species present in Grand Bank plaice were not recorded in the latter paper it was assumed that average phyla values would be appropriate for this presentation. Brawn et al. (1968) calculated a value of 1927 cal/g wet weight for herring with 6.6% fat and 1085 cal/g for cunner. Partly spent capelin contain 3-4% fat (Andrews 1954) and launce probably less than this so that a rough value of 1750 cal/g was used.

Results

Geographic distribution

Plaice were widely distributed throughout the area with some reported from a large proportion of the unit areas. By far the largest number per set was from the Grand Bank surveys particularly the northern half (Div. 3L) (Fig. 3 and 5) although for most localities on the Bank except the southwest slope (Div. 3O) considerable quantities were also taken. It should be pointed out that the southern half of the Bank was subjected to more research sets than any other locality.

The larger numbers indicated for the southern part of St. Pierre Bank and Scotian Shelf (Fig. 3) were probably aberrant values and were each (Fig. 5) from single sets. Three large catches from Bonavista Bay

(P-24 and P-25) also probably fall into this category, although the latter area has supported, in recent years, a fairly good inshore fishery.

Distribution in relation to depth and temperature

Plaice were caught in temperatures from about -1.5 to 5.5°C and from 20 fath (37 m) down to about 400 fath (730) (Fig. 7).

Distribution both in relation to depth and temperature was somewhat different in the two ICNAF Divisions (3L and 3N). In Division 3L (Northern half of the Bank) plaice were generally caught in lower temperatures and shallower water than in Division 3N (Southern half). Catches in excess of 500 fish were caught in temperatures ranging from -1.5 to 1.5°C in Division 3L, however, the greatest percentage of catches of this magnitude occurred between -0.9 and 0°C in 50-100 fath (92-183 m). Some large sets were, however, taken below -1.4°C and at 1.1 to 1.5°C. In Division 3N relatively low catches were recorded below -0.9 and catches of greatest magnitude occurred from 0.4 to 1.5°C at 75-150 fath (139-275 m). Fairly substantial catches were also recorded in the 4.1 to 5.0°C range at 76-100 fath (139-183 m). Generally speaking for both areas, fish taken at deeper locations were in higher temperatures. In the area fished intensively

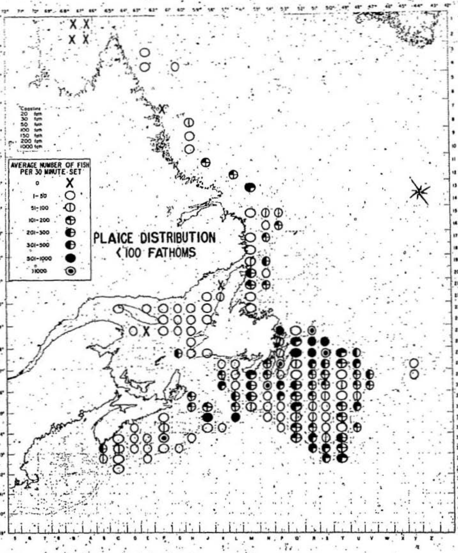

Fig. 3. Catch per 30-min. set of plaice from research vessel cruises in depths 100 fath (183 m) or less. The number of sets involved are shown in Fig. 4.

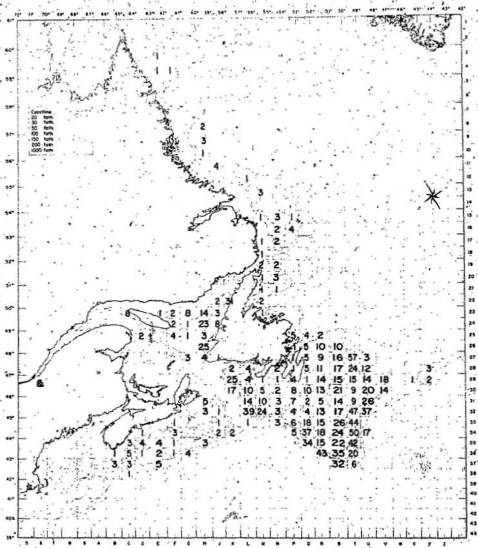

Fig. 4. Number of sets in which plaice were taken in 100 fath (183 m) or less.

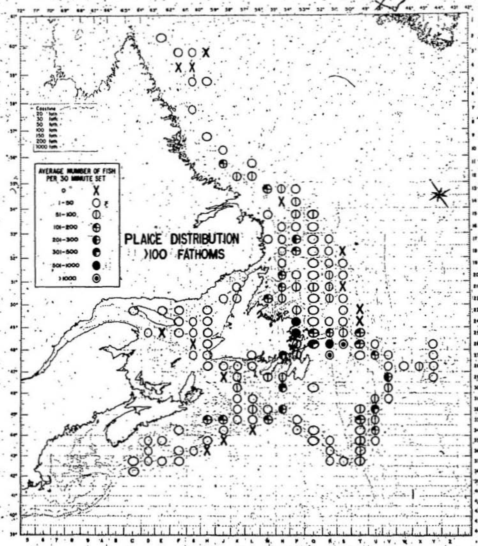

Fig. 5. Catch per 30-min sets of plaice from research vessel cruises in depths ≥100 fath (183 m). The number of sets involved are shown in Fig. 6.

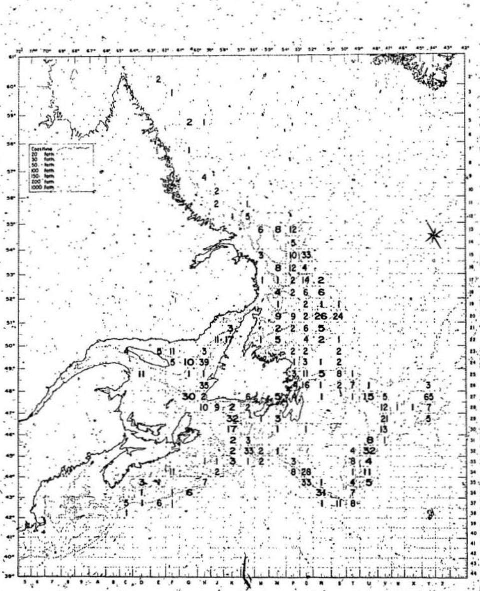

Fig. 6. Number of sets in which plaice were recorded, depths >100 fath (183 m).

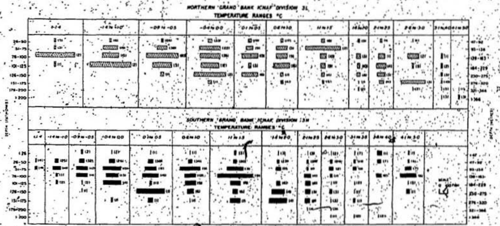

Fig. 7. Distribution of plaice in Divisions 3L and 3N in relation to temperatures and depth.

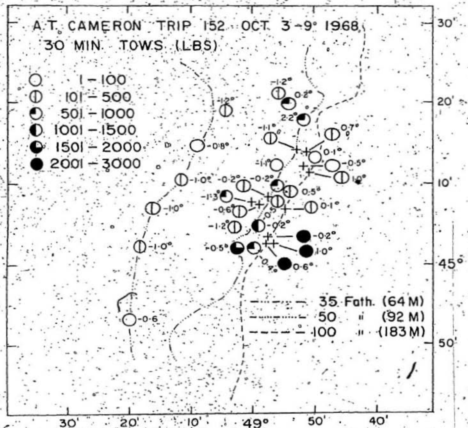

Fig. 8. Record of catches of plaice (weights) and temperatures from a detailed survey of a 30 sq. nautical mile area of the Grand Bank.

on the eastern slope of the Grand Bank (Fig. 8) largest catches occurred at -0.5 to 1.0 °C near the 100 fath (185 m) contour.

Delineation of plaice stocks

(a) Vertebral averages

An analysis of vertebral numbers indicated that, although there was significant heterogeneity throughout the whole Northwest Atlantic from the Labrador to Scotian Shelves (Fig. 9), major differences could not be demonstrated between vertebral samples of plaice caught in the area extending from Division 3K southward over the whole of the Grank Bank. Vertebral averages for this area were significantly higher than averages calculated for the Gulf of St. Lawrence, Labrador Shelf, and Flemish Cap, but none of the Grand Bank averages were significantly different. A vertebral sample from West Greenland (ICNAF 1F) was significantly different from the sample from the opposite side of the Labrador Sea on Hamilton Inlet Bank.

(b) Anal fin rays

Average numbers of anal fin rays were calculated from samples taken from the same localities for which vertebral averages were available. No significant

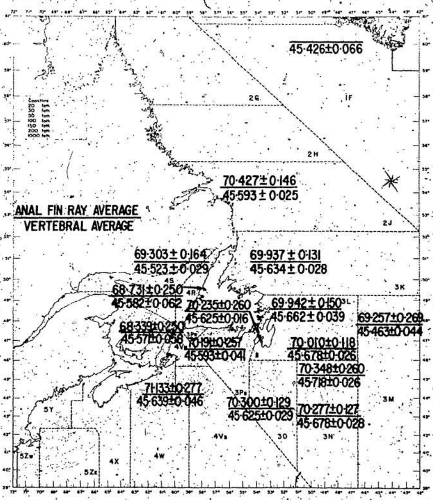

Fig. 9. Anal fin ray, vertebral averages, and standard errors for plaice from certain localities in the Northwest Atlantic.

Table 2. Annal fin ray and vertebral averages together with standard deviation and errors from various localities in the Northwest Atlantic

Locality	FIN RAYS No. in Sample	Average	St. dev.	St. err.	Range	VERTEBRAE No. in Sample	Average	St. dev.	St. err.	Range
1. West Greenland (Div. 1F)						110	45.426	0.623	0.075	44-47
2. Hamilton Inlet Bank (Div. 2J)	394	70.427	2.904	0.146	63-79	713	45.593	0.677	0.025	44-48
3. NE Nfld. Shelf (Div. 3K)	131	69.937	2.769	0.131	60-79	555	45.634	0.665	0.028	44-47
4. Off Bonavista (Div. 3L, north part)	327	69.942	2.707	0.150	62-77	391	45.662	0.605	0.039	44-48
5. N. Grand Bank (Div. 3L)	522	70.010	2.704	0.118	63-80	707	45.678	0.694	0.026	44-48
6. St. Mary's Bay (Div. 3L)	115	70.235	2.785	0.260	63-78	682	45.625	0.668	0.016	44-48
7. E. Grand Bank (Div. 3N)	109	70.348	2.712	0.260	65-77	684	45.718	0.694	0.026	44-47
8. SE. Grand Bank (Div. 3N)	394	70.277	2.534	0.127	62-78	580	45.678	0.666	0.028	42-48
9. SW. Grand Bank (Div. 3O)	443	70.300	2.715	0.129	62-76	480	45.625	0.640	0.029	44-48
10. Flemish Cap (Div. 3M)	109	69.257	2.812	0.269	62-77	220	45.463	0.658	0.044	44-47
11. St. Pierre Bank (Div. 3Ps)	110	70.191	2.886	0.275	64-79	209	45.593	0.598	0.041	44-47
12. Bonne Bay (Div. 4P)	119	68.731	2.732	0.250	60-75	110	45.582	0.655	0.062	44-47
13. S. Gulf of St. Lawrence (Div. 4T)	112	68.[illegible]39	2.646	0.250	62-75	112	45.571	0.611	0.058	44-47
14. N. Gulf of St. Lawrence (Div. 4R)	208	69.303	2.374	0.164	61-65	472	45.523	0.628	0.029	44-47
15. Banquereau (Div. 4Vn)	128	71.133	2.565	0.277	65-77	219	45.639	0.679	0.046	44-47

differences were found between any of the averages for samples taken from localities extending from the NE Newfoundland Shelf (ICNAF Division 3K) over all of the Grand Bank (Divisions 3L, 3N and 3Ø), St. Mary's Bay and St. Pierre Bank (Sub div. 3Ps) (Nos 3 to 9 and 11; Table 2) (Fig. 9). Except for St. Pierre Bank this corresponds to the area of similar vertebral counts in the previous paragraph and as with vertebral averages no significant difference was observed for averages from the three Grand Bank ICNAF Divisions. Anal fin averages from Flemish Cap, the Southern Gulf of St. Lawrence and Banquereau were significantly different from the Grand Bank and adjacent areas.

(c) Tag recovery

More than 70% of the returned tags were from Newfoundland-based trawlers with most of the remainder from Nova Scotia trawlers with returns being generally proportional to the fishing intensity of different trawler groups. The percentages of tag recoveries by trawlers from different countries are shown in Table 3, and a summary of returns from various tagging experiments is given in Table 4.

For all the Grand Bank tagging experiments a substantial percentage of the recaptures was made less than 30 nautical miles from the tagging area (Fig. 10). Very few confirmed recaptures fo long distance migrations were recorded. One plaice tagged on the northeastern slope (Site C, Fig. 10) was caught near St. Mary's Bay,

Table 3. Percentage of tags taken by different countries for the Grand Bank localities shown in Fig. 2 (page 8)

Tagging date and locality	Canada Nfld.	Canada N.S.	France: St. Pierre	Spain	Other European	Total No. returned
(B) Oct. 1954 N. Grand Bank	63.2	36.8	-	-	-	58
(C) June 1961 NE Grand Bank	75.1	19.9	2.0	1.2	1.5	411
(E) June 1961 E Grand Bank	73.8	25.3	0.6	-	0.3	372
(F & G) July 1959 SE & S Grand Bank	78.4	19.3	1.8	-	0.5	219

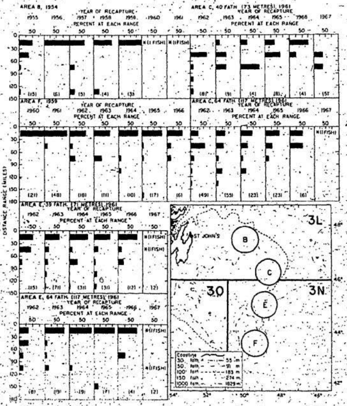

Fig. 10. Percent of recovered tags that were caught in various years at varying distances from the tagging site for a number of tagging experiments. The circles on the map indicates a radius of approximately 30 nautical miles from the tagging position.

Newfoundland, and a fish tagged in the latter Bay was caught on the northeast slope of the Grand Bank. Only 7 recaptures were made from the St. Mary's Bay tagging.

A summary of general migratory patterns is given in Figure 11 and complete details of returns from individual tagging experiments are contained in Pitt (1969).

(d) Growth differences on the Grand Bank

Although differences in growth rate and size at age may not necessarily be indicative of separate stocks, this parameter may indicate that plaice inhabitating different parts of the banks remain in discrete groups following settling or at least at the adult level.

Age-length data collected on random-stratified research cruises in 1973 and 1974 were combined by splitting Divisions 3N and 30 into northern and southern components on an arbitrary basis (Fig. 12). Plaice from the two more southerly groups, 3Ns and 30s, were larger at comparable ages than those from other groups (Fig. 13). The samples from 3L and 30_n produced almost identical growth curves and the curve from 3Nn was intermediate between the curves for the latter areas and those to the south (3Ns and 30s).

Growth

Comparison of growth curves of plaice from a major portion of the Northwest Atlantic is presented in Figure 14

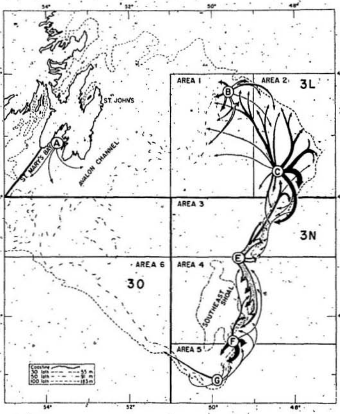

Fig. 11. General migration pattern of plaice tagged on the Grand Bank and in St. Mary's Bay. The areas 1 to 5 were used to tabulate returns for different tagging experiments.

Table 4. Percentages of tags recovered in various years for various tagging experiments. (Letters in the "Locality" column refer to tagging areas in Fig. 2).

Tagging Information					Years after release										
		Depth			0	1	2	3	4	5	6	7	8	9	Total
Locality	Date	fath	m	No.	Percent										%
(A) St. Mary's Bay	June 1954	49-64	90-117	499	-	0.2	0.2	-	0.6	-	-	0.2	-	0.2	1.4
(B) N Grand Bank	Oct. 1954	58-64	106-117	1000	-	2.6	0.7	0.9	0.5	0.4	0.3	0.3	-	0.1	5.8
(C) NE Grand Bank	June 1961	40	73	145	1.4	2.8	4.8	2.8	6.9	1.4	3.5	-	-	-	23.6
" " "	" "	52	95	105	5.7	4.8	11.4	4.8	5.7	3.8	1.0	-	-	-	37.2
" " "	" "	64	117	892	7.5	7.7	8.1	6.8	4.6	1.9	0.6	-	-	-	37.3
(D) E Grand Bank	Sept. 1960	78-80	143-146	83	4.8	2.4	1.2	7.2	3.6	4.8	3.6	1.2	-	-	28.8
(E) " " "	June 1961	39	71	638	3.5	3.1	12.9	8.9	8.0	3.6	1.6	-	-	-	41.6
" " "	June 1961	60	110	324	3.4	2.5	10.2	5.9	4.6	4.6	1.2	-	-	-	32.4
(F) SE Grand Bank	July 1959	50	91	778	1.3	4.2	7.5	3.1	2.0	2.7	3.1	0.9	0.5	-	25.3
(G) S Grand Bank	July 1959	39	71	197	-	2.6	1.0	1.5	2.0	2.0	1.0	-	0.5	-	10.6

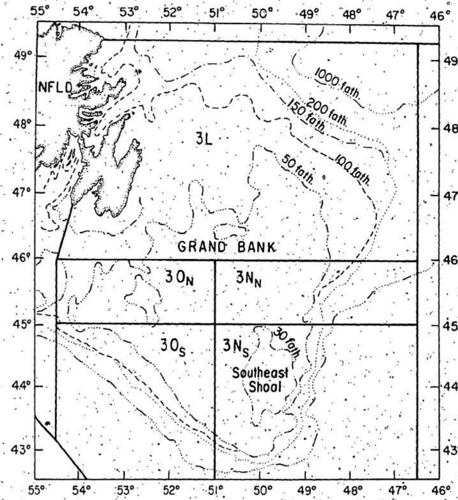

Fig. 12. Splitting of Divisions 3N and 3O into northern and southern components for the purpose of size at age comparisons as shown in Fig. 13.

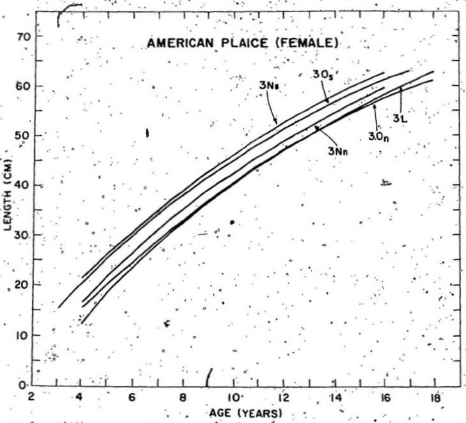

Fig. 13. Growth curves of plaice for a number of Grand Bank localities as shown in Fig. 12.

based on research data.

Growth patterns for Labrador to Bonavista Shelf (ICNAF Division 2H to north part of Division 3L) (Fig. 1) were fairly similar (Fig. 14A). Labrador Shelf plaice were slightly larger at comparable age than the more southerly fish but the difference was not great (Fig. 14A). Growth curves for the Grand Bank showed a gradual decrease in size at comparable age from north to south and around tha tail of the bank to the southwest slope (ICNAF Division 3Ø) (Fig. 14B). Flemish Cap (Division 3M) population has a very rapid initial growth rate (Fig. 14B) possibly because of high bottom temperatures which are prevalent in this area. St. Pierre Bank plaice growth curve is similar to that of the eastern part of the Grand Bank (ICNAF 3L and 3N). Plaice from the small local inshore St. Mary's Bay population (Fig. 14) were generally smaller in length at comparable ages than those from other localities considered here.

To show differences between localities the average size at age 5 and 15 was selected. Positive significant correlations were found between average bottom temperature and these average sizes for the different areas for which data were available (Fig. 15) ($r = 0.943$ for 5 years and $r = 0.819$ for 15 years $P<0.001$ in both cases). The large size for 15-year-olds from Flemish Cap (ICNAF Division 3M) is perhaps because plaice in this locality have a rapid initial period of growth but the rate of increase is reduced at a comparatively early age so that the rate of growth for ages 6-8 onwards is lower than those from the southwest slope of the Grand Bank (No. 10).

The Northeast (Division 3L (No. 7) and East (Divisions 3L and 3N) (No. 8) Grand Bank samples and St. Mary's Bay (No. 11) are relatively close in the 5-year comparisons (Fig. 13A); however, at age 15 the position of nos. 7 and 8 are changed in relation to St. Mary's Bay (No. 11) because of an increase in the rate of growth of the two Grand Bank areas after age 5. The plaice from southern Grand Bank areas (Nos. 9 and 10) apparently grew at a more rapid rate than those to the north, except those from Flemish Cap, at least up to age 15.

Spawning and Maturity

(a) Spawning season

The peak spawning period ranged from early April for Flemish Cap (Division 3M) to early June for Labrador-Northwest Newfoundland Shelf (ICNAF Divisions 2H, 2J and 3K). For the Grand Bank, (Divisions 3K, 3N and 3O) spawning occurred from early April to mid-May (Fig. 16) (Pitt 1966).

(b) Spawning grounds

No specific spawning ground for this species was

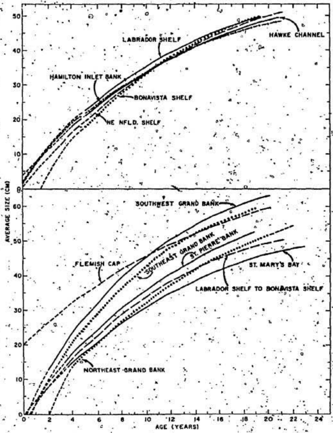

Fig. 14. Growth curve comparisons of plaice for a number of locations in the Newfoundland area of the Northwest Atlantic. (See locations Fig. 1) (Fitted Betalanffy Curves)

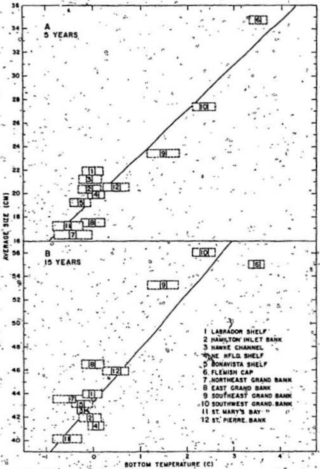

Fig. 15. Lengths at (A) age 5 and (B) age 15 of female plaice in relation to average bottom temperature (solid rectangles) and probable temperature range (broken rectangles)

recognized partly because a large proportion of the area was covered by drift ice from the middle of March to late May, making it impossible to have a complete coverage of all localities during the spawning season. A study of fishing records from commercial trawlers and limited research vessel data did not reveal any unusually large concentrations of American plaice during the spawning period from any particular locality. This does not preclude the possible existence of certain areas where a combination of environmental conditions, such as type of bottom, temperature, and depth, is especially suitable for the spawning activity of this species. Most of the northeastern and eastern slopes of the Grand Bank support the largest concentrations of American plaice in the Northwest Atlantic and these regions are also areas of greatest spawning activity.

From many surveys of the Northwest Atlantic by research vessels operated by the Newfoundland Biological Station, it was evident that spawning of American plaice was widespread, with the Grand Bank and to a lesser extent the southern half of the Gulf of St. Lawrence supporting the main spawning populations. American plaice also spawn on Hamilton Inlet Bank, the Northeast Newfoundland Shelf, St. Pierre Bank, and the banks off Nova Scotia. In addition, it is likely that plaice spawn on the remainder

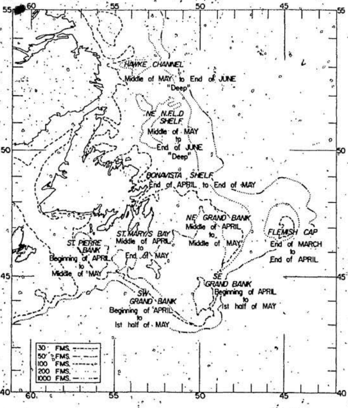

Fig. 16. Map of the area indicating probable spawning time of plaice in a major proportion of the Northwest Atlantic.

of the continental shelf from Davis Strait southward along the Labrador coast and around the coast of Newfoundland and into most of the colder bays, principally at depths to about 100 fath (183 m).

(c) Age and length at sexual maturity

Age at 50% Maturity - Females - Except for Flemish Cap M_{50} for all areas ranged between 12.17 and 15.15 years (Table 5 and Fig. 17). The Flemish Cap population (M_{50} = 7.76 years) matured about 4 years earlier than those of the other areas ($P<0.001$). For the Southeast Grand Bank M_{50} (12.17) was lower than for all remaining areas ($P = 0.001$). For the Southwest Grand Bank (13.63), the Northeast Grand Bank (13.98), and St. Pierre Bank (14.21) the values did not differ from one another ($P > 0.05$). Values for Northeast Newfoundland Shelf-Hawke Channel (14.79) and St. Mary's Bay (15.15) were not different from each other ($P>0.05$) but were different from those for all other areas ($P<.01$). Flemish Cap samples contained mature specimens at 6 years whereas for remaining areas first mature fish were found at 9-11 years. Rates at which females became sexually mature (slopes) did not differ between areas ($P<0.05$).

Males - Males became mature between 3 and 13 years, and M_{50}s were heterogeneous. The range was

5.33- 7.48 years (Table 5 and Fig. 17), but data were not available for Flemish Cap. Values for Northeast Grand Bank (7.33) and St. Pierre Bank (7.48) did not differ (P => 0.5) but both were higher than those for the other four areas. For these areas only the Southeast (5.32) and Southwest (5.46) Grand Bank values were not different (P => 0.5).

Length at 50% Maturity - Lengths at 50% maturity were taken from age-length curves using the M_{50} for age, and were listed as follows (in centimetres):

	Northeast Nfld. Shelf and Hawke Channel	St. Mary's Bay	Grand Bank North-east	Grand Bank South-east	Grand Bank South-west	St. Pierre Bank	Flemish Cap
Males	24.4	20.0	24.0	24.8	29.3	27.8	...
Females	42.8	40.2	42.6	46.8	53.6	44.6	41.3

The lower size ranges for the males were perhaps not adequately sampled in some areas. Length at 50% maturity for males and females ranged from 20.0 and 40.2 cm for St. Mary's Bay to 29.3 and 53.6 cm for the Southwest Grand Bank. Both St. Mary's Bay and Flemish Cap females began to mature at approximately the same size, although there was a great difference in their ages at comparable sizes.

Table 5. Details of results of calculation mode for age at M_{50} for various localities.

Area	Sex	M_{50} (years)	Log. Line Slope	Fit of Line X^2	df	χ^2 ($P_{.05}$)
NE Shelf	M	6.470 ± 0.210	9.686 ± 1.025	4.094	5	11.070
	F	14.791 ± 0.224	15.747 ± 1.407	5.130	5	11.070
St. Mary's Bay	M	5.811 ± 0.112	7.600 ± 0.431	12.322	8	13.362
	F	15.151 ± 0.163	15.189 ± 1.007	10.590	6	12.592
N. Grand Bank	M	7.329 ± 0.186	7.451 ± 0.873	4.249	6	12.592
	F	13.982 ± 0.232	17.774 ± 2.130	4.180	6	12.592
Flemish Cap	M	---	---	---	-	---
	F	7.760 ± 0.236	15.692 ± 2.976	3.80	1	3.840
SE Grand Bank	M	5.321 ± 0.129	9.905 ± 0.914	9.265	4	9.488
	F	12.173 ± 0.150	13.398 ± 1.074	6.591	6	12.592
SW Grand Bank	M	5.461 ± 0.080	8.408 ± 0.505	8.941	6	12.592
	F	13.630 ± 0.238	15.108 ± 1.946	3.000	6	12.592
St. Pierre Bank	M	7.480 ± 0.227	8.918 ± 1.025	7.495	6	12.592
	F	14.211 ± 0.286	14.553 ± 1.974	1.913	6	12.592

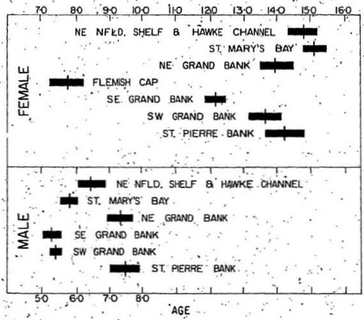

Fig. 17. Age at which 50% of plaice are mature from various localities. The vertical bar is the mean and the rectangles the limits of twice the standard error of the mean.

Fecundity

Fecundity of this species was related to length, weight and age. In all cases it was found that a double logarithmic transformation gave linear relationships.

(a) Fecundity and fish length (Fig. 18)

Using the data from all samples fecundity was found to increase with length to the following relationship:

$$F = 0.002103L^{3.1709}$$

where F = fecundity in thousands of ova, and L = length in centimetres. The correlation coefficient (r) was highly significant = 0.874 $P < 0.001$.

(b) Fecundity and fish weight (Fig. 19)

Log fecundity plotted against log gutted weight (in grams) gave the relationship

$$F = 1.094W^{0.9011}$$

where W = gutted and gilled weight in grams, r = 0.810; $P = < 0.001$.

(c) Fecundity and age (Fig. 20)

Fecundity on age was presented to show the wide scatter of points. This was to be expected since fish from a number of locations with widely divergent size at age relationship were included here. The equation of fecundity on age using data from all localities was as follows:

$$F = 21.71t^{1.1781}$$

where t = age in years.

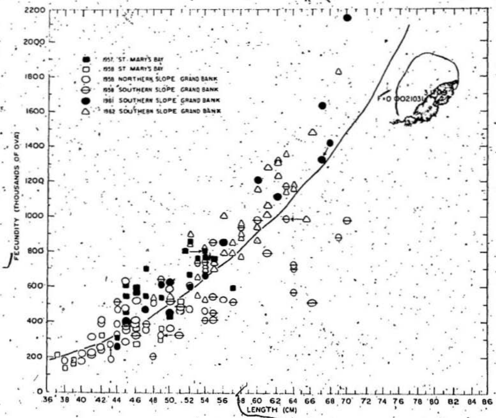

Fig. 18. Scatter diagram of American plaice fecundity plotted against length and the fitted regression line.

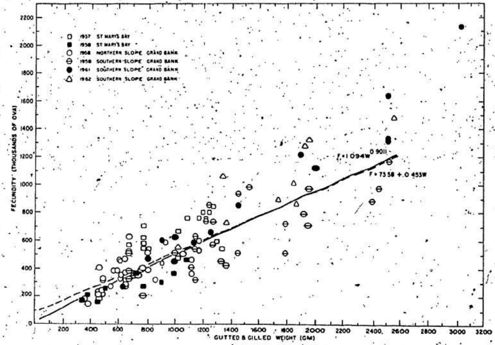

Fig. 19. Scatter diagram of American plaice fecundity plotted against gutted and gilled weight and the fitted regression lines for the arithmetic and log-log values.

(d) Comparison of fecundity and length for three areas

For the three areas from which samples were taken the following equations have been calculated (F being in thousands of ova in all cases):

(i) St. Mary's Bay. Log F = 3.7944 Log L - 3.7090 (28 specimens)

(ii) Northern slope of the Grand Bank.
Log F = 2.6773 Log L - 1.8602 (32 specimens)

(iii) Southern slope of the Grand Bank.
Log F = 3.0382 Log L - 2.4445 (80 specimens)

An analysis of covariance indicates that there is no significant difference either between slopes ($F = 1.60$ for $F_{05} = 3.07$) or adjusted means of log fecundity plotted against log length for these three areas ($F = 0.63$ for $F_{05} = 3.07$), in spite of the fact that plaice from the southern slope of the Grand Bank are larger at comparable ages and mature at larger sizes than those of the other two areas.

Comparing samples for the same year (1958) from the northern and southern slopes of the Grand Bank also indicates no significant differences between slopes (rate of fecundity increase) ($F = 1.25$ for $F_{05} = 4.07$) or adjusted means ($F = 0.50$ for $F_{05} = 4.07$).

(e) Comparison of years

A comparison was made between the fecundity-length

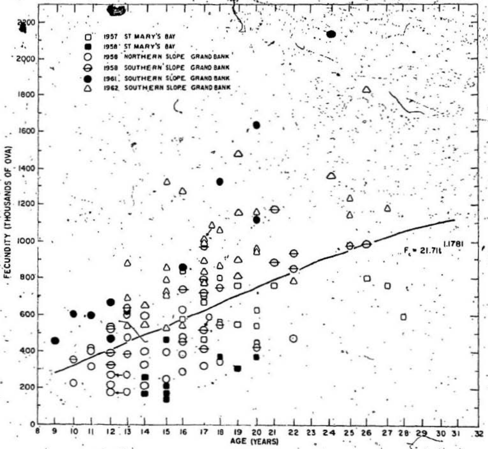

Fig. 20. Scatter diagram of American plaice fecundity plotted against age and the fitted regression line.

relationships of samples for 4 different years. Rates of fecundity increase are significantly different at the 5%, but not at the 1% level ($F = 4.09$ for $F_{05} = 2.84$ and $F_{01} = 4.31$). This suggests the possibility of differences in the number of eggs produced in different seasons. However, some samples were comparatively small, e.g. 18 for 1957 and 14 for 1961. The various relationships are summarized in Table 6.

Food and feeding

Diet composition

Invertebrates, principally benthic forms, occurred most frequently in plaice stomachs with fish being next in frequency of occurrence, but, as a percentage of total food weight, fish far surpassed all other groups (Fig. 21 and Table 7B).

Echinoderms were the principal invertebrate group and were represented almost entirely by brittle stars (Ophiuroidea), sand dollars and sea urchins (Echinoidea). Representatives of the main orders of Crustacea occurred but were dominated by the Amphipoda, Euphausiacea, Cumacea and Decapoda. Most of the molluscs were bivalves (Pelecypoda). Fish consisted almost entirely of sand launce, Ammodytes dubius, and capelin, Mallotus villosus.

Table 6. Summary of relationships between fecundity and length, gutted weight, and age.

Log fecundity in relation to	Intercept (a)	Regression coefficient (b)	Correlation coefficient (r)	Test of statistical significance
Log length (all areas)	2.6772	3.1709	0.874	P=<0.001
Log (gutted and gilled) weight (all areas)	0.0380	0.9011	0.872	P=<0.001
Gutted[a] and gilled weight (all data)	73.59	0.453	0.810	P=<0.001
Log age (all areas)	1.3367	1.1781	0.478	P=<0.001
Log age (northern area)	1.4228	0.9599	0.473	P=<0.01
Log age (southern area)	1.5050	1.1403	0.705	P=<0.001

[a] Fecundity against weight.

Food variation between areas

Disregarding fish size for the moment, echinoderms occurred in significantly more stomachs in the northern samples (Division 3L) than in those from the southeast (Division 3N) ($P = < 0.0001$) (Fig. 21 and Table 7). Echinoderms also accounted for a significantly higher proportion of the total weight in Division 3L than in 3N, ($P = < 0.0001$). Brittle stars (Ophiuroidea) (33.3%) occurred most frequently of all the organisms recorded in Divisions 3L followed by the sand dollars and sea urchins (Echinodea). Both of these groups occurred in significantly greater proportions in Division 3L than in Division 3N ($P < 0.01$). Significantly more fish in Division 3L also contained molluscs and annelids ($P = < 0.03$) and these accounted for significantly higher proportions of total food taken.

Fish and Crustacea, the two other major food groups, were represented in significantly higher proportions in the southeast areas (Division 3N) ($P < 0.01$), however, quantities taken were relatively small in both areas. Fish occurred in 29.6% of the Division 3N stomachs and accounted for 83% of the total weight of food. Both of these percentages were significantly different from Division 3L ($P < 0.001$) where fish occurred in only 9.1% of the stomachs and accounted for 51.9% of the total weight. Significantly more plaice were found containing capelin (Mallotus) in

Division 3L (5%) than in 3N (3%) ($P = < 0.01$) and capelin accounted for 20% of the food as compared to about 6% in the southeast area ($P = < 0.001$). Sand launce (Ammodytes), however, were much more important in Division 3N, occurring in 27.8% of the stomachs and accounting for over 80% of the total food weight against an occurrence of 4.2% and about 30% of the total weight in Division 3L ($P < 0.001$ in both cases). There were significantly more empty stomachs in Division 3L ($P < 0.002$).

Taking size of fish into consideration (Fig. 22 and Table 7), the same general pattern was observed as for all sizes combined (Fig. 21). In Division 3L echinoderms, molluscs and annelids were selected by significantly more fish in nearly all size groups. In Division 3N, however, although echinoderms were still important, fish and crustaceans were selected more frequently by all size groups in which they occurred. No fish, molluscs or annelids were selected by the 10-cm group in Division 3N (Table 7).

Except for significantly higher percentage by weight of capelin in the 20-29 and 30-39 cm groups in Division 3L the distribution by weight followed roughly the pattern as the occurrence (Table 7). Generally greater percentages by weight of echinoderms, molluscs and annelids were found in Division 3L and significantly greater

Table 7. Detailed comparison of the (A) percent occurrence and (B) percent of total weight of food for each length-group for the various food types, ICNAF Divisions 3L and 3N. Asterisks indicate significantly greater amounts at the 5% level. Percent occurrence calculated from total no. examined.

(A) Percent occurrence

	10–19 cm		20–29 cm		30–39 cm		40–49 cm		50–59 cm		60–69 cm	
Food type	3L	3N	3L	3N	3L	3N	3L	3N	3L	3N	3L	3N
Coelenterata	0.9	–	0.9	0.6	2.0	0.9	1.9	1.3	1.8	1.7	–	2.1
Porifera	–	–	0.2	0.6	–	0.9	0.2	0.7	0.3	0.2	–	–
Echinodermata	17.5	8.3	32.1*	26.0	47.6*	29.9	47.3*	25.9	47.6*	26.8	55.6*	32.0
Asteroidea	–	–	–	–	–	0.1	0.2	0.1	0.3	–	–	–
Ophiuroidea	17.5	12.5	28.7	21.5*	37.2*	21.2*	35.2*	19.2	32.6*	18.6	41.3*	16.4
Echinoidea	–	–	4.5	8.0*	15.7*	11.5	23.8*	10.7	25.4*	13.2	30.4	31.6
Crinoidea	–	–	–	–	–	0.1	–	0.3	0.3	–	–	–
Holothuroidea	–	–	–	–	0.2	–	–	–	–	–	–	–
Mollusca	–	–	2.2	1.4	4.7*	2.7	11.6*	2.6	9.5*	3.3	10.8	9.3
Pelecypoda	–	–	2.0	1.2	4.6*	2.6	5.6*	2.0	9.0*	2.5	10.9	8.2
Cephalopoda	–	–	–	–	–	–	–	0.1	–	–	–	–
Gastropoda	–	–	0.2	1.05	0.3	0.1	0.3	0.5	0.6	0.8	–	1.0
Scaphopoda	–	–	–	–	–	–	–	–	0.3	–	–	–
Annelida	13.9*	–	10.8*	2.5	10.5*	3.7	9.6*	2.1	7.5*	2.7	4.3	2.1
Polychaeta	13.9*	–	10.8*	2.5	10.3*	3.7	9.4*	2.1	7.2*	2.7	4.3	2.1
Gephyrea	–	–	–	–	0.2	–	0.2	–	0.3	–	–	–
Unidentified	–	–	–	–	–	–	–	–	–	–	–	–
Crustacea	20.4	29.2	23.1	45.9*	16.2	40.5*	11.4	27.8*	7.8	15.3*	4.3	14.4*
Amphipoda	9.3	25.0*	9.6	27.5*	6.4	20.5*	2.2	6.7*	0.6	4.4*	–	1.0
Cumacea	6.4	4.2	8.7*	3.5	6.6*	1.7	2.9*	0.3	1.5*	–	–	–
Copepoda	–	–	–	0.2	–	0.1	–	–	–	–	–	–
Decapoda	–	–	2.9	1.0	2.9*	0.7	5.6*	1.2	4.8*	0.8	2.1	4.1
Isopoda	–	–	0.7	6.4*	1.6	9.9*	1.3	8.2*	0.9	6.1*	2.2	1. 0
Euphausiacea	5.6	–	3.4	19.0*	0.8	19.1*	0.3	16.2*	–	6.7*	–	8.2*
Mysidacea	–	–	–	–	–	0.2	–	–	–	–	–	–
Other Inv.	1.9	–	1.1	–	0.8	0.7	0.5	0.2	0.9	0.4	–	–
Ascidian	–	–	–	–	<0.1	–	–	–	–	–	–	–
Pisces	–	–	3.4	3.5	7.6	22.7*	15.5	40.4*	11.7	49.4*	6.5	33.0*
Mallotus	–	–	1.8	0.6	5.1	3.7	9.0*	2.9	4.2	4.0	–	5.2
Ammodytes	–	–	0.4	1.0	2.1	17.1*	7.7	37.9*	8.0	46.4*	6.5	28.9*
Other	–	–	1.1	1.7	0.5	2.4*	0.2	0.9	–	0.2	–	1.0
Sand, stones, and plants	0.9	4.2	–	–	0.3	0.1	1.5	–	2.7*	0.4	0.1	–
Unidentified	0.1	–	0.1	0.1	–	–	–	–	–	–	–	–
Empty	46.3	66.7	38.3	33.9	34.1*	28.2	32.0	28.5	32.3	26.9	30.4	26.8
No. of stomachs	108	24	446	484	630	862	594	907	334	478	46	97
or wt of contents	–	–	–	–	–	–	–	–	–	–	–	–

(B) Percent of total weight at each size-group

	10–19 cm		20–29 cm		30–39 cm		40–49 cm		50–59 cm		60–69 cm	
Food type	3L	3N	3L	3N	3L	3N	3L	3N	3L	3N	3L	3N
Coelenterata	0.1	–	0.9	0.2	1.3*	0.5	0.6	0.4	0.7	0.6	–	6.5*
Porifera	–	–	0.3	0.3	–	0.1	<0.1	<0.1	–	<0.1	–	–
Echinodermata	23.2	18.2	28.1*	11.2	32.4*	8.7	23.1*	6.3	36.2*	7.2	52.5*	13.8
Asteroidea	–	–	–	–	–	–	0.1	–	<0.1	–	–	–
Ophiuroidea	23.8	–	23.6*	7.4	20.5*	4.4	10.7*	3.4	13.1*	3.5	20.2	5.2
Echinoidea	–	–	4.8	3.8	12.1*	4.3	12.7*	2.9	23.2*	3.7	32.0	8.4
Crinoidea	–	–	–	–	–	–	–	–	<0.1	–	–	–
Holothuroidea	–	–	–	–	<0.1	–	–	–	–	–	–	–
Mollusca	–	–	2.4*	0.5	2.7*	0.5	6.1*	0.6	5.6*	0.7	21.7*	3.0
Pelecypoda	3.7	–	2.3*	0.5	2.4*	0.5	5.4*	0.5	5.5*	0.6	21.7*	2.9
Cephalopoda	–	–	–	–	–	–	–	<0.1	–	–	–	–
Gastropoda	–	–	<0.1	–	0.3*	<0.1	0.7*	<0.1	<0.1	0.1	–	<0.1
Scaphopoda	–	–	–	–	–	–	–	–	<0.1	–	–	–
Annelida	26.4	–	11.3*	0.6	5.0*	0.4	1.6*	0.1	1.0*	0.1	0.3*	<0.1
Polychaeta	26.4	–	11.3*	0.6	5.0*	0.4	1.5*	0.1	1.0*	<0.1	0.3*	<0.1
Gephyrea	–	–	–	–	<0.1	–	0.1	–	<0.1	–	–	–
Unidentified	–	–	–	–	–	–	–	–	–	–	–	–
Crustacea	42.0	72.7	30.8	71.6*	4.5	24.0*	4.9	7.5*	8.9*	1.7	3.7	4.9
Amphipoda	9.7	–	8.1	10.4	1.3	2.3*	0.1	0.4*	<0.1	0.1	–	0.2
Cumacea	14.1	–	5.7*	1.3	0.8	<0.1	<0.1	<0.1	<0.1	–	–	–
Copepoda	–	–	–	<0.1	–	<0.1	–	–	–	–	–	–
Decapoda	–	–	10.3*	2.1	2.1*	0.5	4.2*	1.0	8.9*	0.7	3.7	2.9
Isopoda	–	–	0.2	1.2	–	–	<0.1	–	<0.1	–	0.6	–
Euphausiacea	19.4	–	6.8	57.1*	0.1	20.3*	0.5	5.4*	–	0.7*	–	1.7*
Mysidacea	–	–	–	–	–	0.2	–	–	–	–	–	–
Other Inv.	2.2	–	0.9	–	<0.1	0.1	0.1	<0.1	0.2*	<0.1	–	–
Ascidian	–	–	–	–	<0.1	–	–	–	–	–	–	–
Pisces	–	–	24.8*	14.9	53.3	65.3*	61.6	84.8*	46.1	89.6*	21.8	77.2*
Mallotus	–	–	14.3*	2.2	38.4*	8.5	29.8*	4.6	11.4*	6.0	–	10.1*
Ammodytes	–	–	7.6	9.7	14.1	54.3*	32.4	79.5*	34.9	83.2*	21.6	67.1*
Other	–	–	3.1	2.8	1.1	2.4	0.4	0.6	–	0.1	0.3	0.1
Sand, stones, and plants	<0.1	–	0.1	0.1	<0.1	–	0.3	–	0.9	–	0.3	–
Unidentified	<0.1	–	<0.1	<0.1	–	–	–	–	–	–	–	–
Empty	–	–	–	–	–	–	–	–	–	–	–	–
No. of stomachs	–	–	–	–	–	–	–	–	–	–	–	–
or wt of contents	13.4	1.1	193.8	486.5	1109.8	3516.9	3738.2	11352.3	3164.7	12705.2	744.2	3055.2

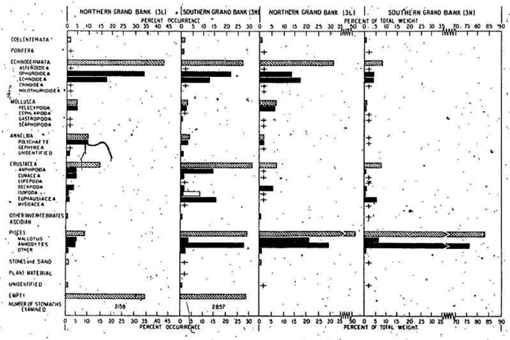

Fig. 21. Diet comparisons of plaice in ICNAF Divisions 3L and 3N. Percent occurrence calculated from total number of fish examined for each Division and percent of total weight calculated from total weight of food for each Division (Phyla or other totals cross-hatched, + = < 1.0%).

percentages of fish and crustaceans in Division 3N. The distribution by weight of echinoderms and molluscs remained roughly the same at all sizes. However, an increase in the consumption of fish with predator size was coupled with the opposite trend for crustaceans (Fig. 22). Except for the 10-19 cm group in Division 3L, annelids were taken in relatively small quantities.

Caloric value of stomach contents

Log-log regression of mean caloric value per 100 fish versus fish size (mid-point of the 10-cm length group) were made and covariance tests performed for seasonal data and for the total of each ICNAF Division (Fig. 23). The rate of increase with length in the caloric value of stomach contents per 100 fish examined indicated a similarity between data collected for the two ICNAF Divisions during the April-June period only ($F = 0.81$ and 0.01 for slope and adjusted means respectively for $F_{05} = 5.12$). For the other two periods and for the totals, an analysis of covariance indicated significant differences between the regression coefficients for the two Divisions ($F = 6.38$ for July-September, 15.39 for October and November and 8.40 for the totals for $F_{05} = 5.12$) with the values being lower for Division 3L than for 3N.

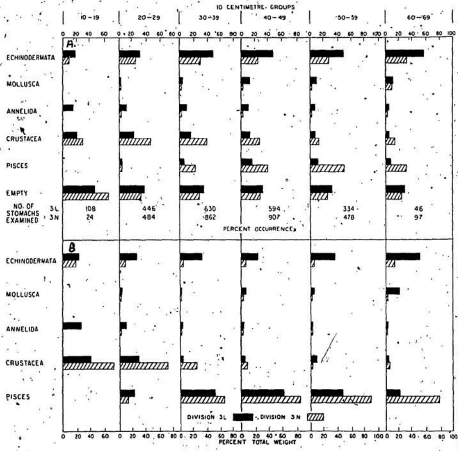

Fig. 22. Percent occurrence (A) and percent of total food weight (B) at various size groups for the major food components of plaice from ICNAF Divisions 3L (solid) and 3N (hatched). Occurrence = (no. of fish in which item appeared/total no. examined at each size category) x 100. Percent total weight = (weight of particular item/total wt. of food for size category) x 100.

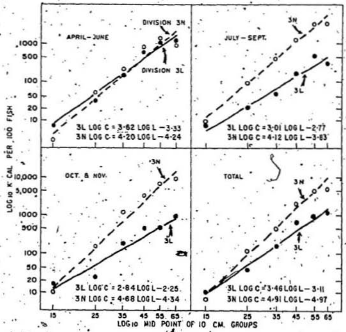

Fig. 23. Unweighted log-log regressions of kcal per 100 fish examined on mid-point of length group for monthly periods shown and also annual totals.

DISCUSSION

Distribution

According to Norman (1934) one species, Hippoglossoides platessoides, is recognized in the North Atlantic with two subspecies each with its own geographic range. The European subspecies, Hippoglossoides platessoides limandoides (Bloch) (commonly called the long rough dab) is found along the coast of northeast Europe from the vicinity of Novaya Zemlya (Milinski 1944), the Barents Sea, Spitzbergen southward into the Baltic, around the British Isles and as far west as Iceland. The Northwest Atlantic subspecies, H. platessoides platessoides (Fabricius), the American plaice, has a distribution extending from Greenland to Cape Cod.

The European subspecies appears to be generally smaller than the North American subspecies and Bagenal (1955) showed that specimens from the Clyde Sea area rarely grew beyond 30 cm and none were found older than six years, compared to ages up to 25+ and greater than 60 cm in the Northwest Atlantic. Some of this of course is probably a function of temperature which might have accelerated the growth process with fish maturing very early and reaching their asymptotic size at a relatively young age. It seems possible that Icelandic and Barents Sea populations may be intermediate forms.

Plaice are distributed through the Newfoundland area and a high proportion of the fishing sets through the area produced at least some specimens. The symbols in Figures 3 and 5, while giving some indication of density, may be a little misleading in this respect since frequently they represent single sets only. The Grank Bank is the location of greatest plaice density and is the location of the largest commercial fishery for this species in the Northwest Atlantic.

It is a "cold" water species and appears to prefer water temperatures of approximately 1°C to -1°C and depths ranging from 50-150 fath (92-275 m). However, in relating distribution and abundance of plaice to temperature and depth, it is possible that the bottom type may be important and the preference for grain size could take precedence over the influence of temperature. Unfortunately, we have no data on which to base conclusions in this respect.

Stock Delineation

Generally, vertebral and fin ray counts were not particularly useful in delineating American plaice stocks on the Grand Bank. There could be a number of contributing factors such as a small inherent variability of meristic parts, so that when a number of year-classes were combined, differences in fin rays or vertebral numbers resulting from the influence of varying environmental conditions may have canceled each other out. Then also with a relatively long spawning period there could be a range of environmental conditions influencing developing embryos throughout the spawning period.

Because of the lack of wide meristic differences, it is suggested that American plaice in all of ICNAF Subarea 3 with the exception of Division 3M (Flemish Cap) either belong to a single stock or have considerable intermingling at least during egg and larval stages.

Tag recoveries even up to seven years after release were mostly from locations less than 30 miles (48 km) from the release locality. There was no evidence of substantial migrations between bank areas and Newfoundland inshore localities; however, up to 1964 there was only a relatively small inshore plaice fishery and this would probably preclude recoveries from the 1954 tagging on the northern part of the Grand Bank (area 1 Fig. 2) if indeed plaice did move inshore.

Most fish migrations are associated with spawning or feeding patterns or with changes in environmental conditions or perhaps a combination of all three. On the slopes of the Grand Bank, a variety of temperature and feeding conditions is available, thus requiring very little movement for plaice to find their preferred temperature when conditions change. Although plaice make limited diurnal movements (Pitt 1967), it seems doubtful that they pursue pelagic food species for great distances and therefore there is no large mass movement as is evident for cod when the latter follow capelin towards the Newfoundland coast although as indicated elsewhere plaice do feed extensively on capelin. Plaice, as indeed all flatfish, species are intimately associated with the benthic environment.

On the basis of meristic and tagging information, it seems probable that very minimal intermingling of adult plaice between geographic regions occurs, and instead of large aggregate populations in the Northwest Atlantic and on the Grand Bank in particular, they occur in randomly distributed groups, intermingling between groups occurring to a large extent only in the egg and larval stages. The similarity of anal fin ray and vertebral counts in most of ICNAF Subarea 3 supports the possibility of intermingling in the early life stages.

In terms of numbers of spawning fish the largest groups occur on the Grand Bank, however, spawning also occurs throughout the Northwest Atlantic from Davis Strait to Georges Bank including the coast of Newfoundland.

Bigelow and Schroeder (1953) stated that incubation of plaice eggs in the Gulf of Maine occupied 11-14 days at about 4°C. Obviously, lower temperatures such as those occurring in April and May in the Newfoundland area would extend the period of larval development. Metamorphosis, which in the Gulf of Maine occupies 3 - 4 months, would extend over a longer period in northern areas, hence egg and larval drift would be quite extensive. Since southward current velocities are about 4 - 5 knots to the east of Labrador and Newfoundland, many eggs and larvae from the Labrador Shelf, Hamilton Inlet Bank and the Northeast Newfoundland Shelf could be transported to the Grand Bank. By the same process, eggs and larvae from the latter area could be swept beyond the continental shelf.

Frost (1938) found early stage eggs and larvae in September over the northern half of the Grand Bank and northward to the Strait of Belle Isle. The latter author suggested that Grand Bank was stocked from spawning in northern areas with the latter in turn receiving recruitment by larval drift from West Greenland and migrations from the south. In view of apparent limited movement of Grand Bank plaice, the latter appears to be most unlikely. West Greenland does support an apparently small plaice population and also vertebral averages from this locality were similar to those from the Labrador Shelf. There is at present no evidence of larval drift across the Labrador Sea.

Although the southward flow especially east of

Hamilton Inlet Bank and the Northeast Newfoundland Shelf is quite strong, Nevinsky and Serebryakov (1972) found plaice eggs and larvae together along the continental shelf from Labrador to the Grand Bank. They suggested that, whereas there are high velocity currents in the Hamilton Inlet Bank-Northeast Newfoundland Shelf areas, there is sufficient eddying to retain a substantial proportion of the larvae in the spawning area. On the Grand Bank, however, because current velocities were lower they concluded from the distribution of eggs and larvae in the vicinity of spawning areas, that loss beyond the continental shelf was minimal.

The probable pattern of egg and larval drift coupled with meristic data then seem to indicate a certain degree of intermingling during early stages of plaice from spawning in different localities. However, once the larvae have metamorphosed and settled, they probably make minimal movements although there could be a gradual segregation according to size and stage of maturity within localized areas. Differences in the growth curves (Fig. 13) for different areas of the Grand Bank seems to support this.

Since the major fishery for plaice occurs on the Grand Bank the delineation of stocks is most important here. At present the whole of the bank is managed as a single stock with a total aggregate Total Allowable Catch allocated although the basis of the stock assessment was by ICNAF Division (Section 2).

When the ICNAF Divisions were drawn up in the late 1940's the main interest on the Grand Bank was haddock and cod and the lines separating divisions were drawn to suit these species to a great extent. On the basis of the tagging studies, it appears that a correct division of plaice on the eastern and northeast parts of the Grand Bank would be into 3 groups (Fig. 11) (also Fig. 12) (a) northern group comprising the north and northeast slopes, (b) a southern group, and (c) a central group between (a) and (b) receiving some migrations from both north and south, but with possibly more intermingling from the southern group. Additionally, the western side (Division 3O) of the bank could be split into southern and northern components. However, the ICNAF divisions do separate the nothern and southern portions of the bank at least and fisheries statistics are presently only available by these divisions. However, some difficulty arises within-division differences in size at age when using average sizes to convert weights to numbers etc., when the samples are not spread over the whole division.

Sexual Maturity and Spawning.

Time of spawning

The generally accepted idea is that reproduction activity is controlled by pituitary hormones with this gland, in fish at least, being stimulated by certain external environmental factors. There is not complete agreement as to which factors are important and how they act. Atz and Pickford (1964) gave an extensive bibliography on the pituitary gland and its relation to reproduction of fishes.

Temperature is the factor for which information is available to any degree, but was not available for all spawning areas during the spawning season. The effects of temperature on the maturing gonads may be indirect - resulting from a reduction in feeding at low temperatures. Kohler (1964) showed that cod ate less food at low temperatures; he also showed that when food supplies were low, cod failed to complete the maturity process.

Spawning plaice were taken from near bottom water temperatures from -1.5°C for the northern Grand Bank to above 3°C for Hawke Channel, the Northeast Newfoundland Shelf and Flemish Cap. Nevinsky and Serebryakov (1973) reported the most intensive spawning at 0° to 2.5°C in the Northwest Atlantic.

The effects of light on maturation of marine fish is not as well known because of the technical difficulty of measuring light at various depths. Plaice are generally bottom dwellers, but some apparently leave the bottom at night. Plaice to the north in the areas off Labrador and Northeast Newfoundland Shelf spawn later than those from the Grand Bank in spite of the fact that they are probably in higher temperatures.

Time of spawning determined by Nevinsky and Serebryakov (1973) generally agreed with those presented here and Pitt(1966), although for the two Grand Bank areas and St. Pierre Bank they reported some spawning as early as February and for a number of localities they indicated a longer spawning period than reported here. This was perhaps because their determination of maturity stages was slightly different from the method used here and their judgment of when the peak period was completed could also be at variance with that presented here.

Age and size at sexual maturity

According to Bagenal (1957) the European subspecies: H. platessoides limandoides, females are 50% mature between their 2nd and 3rd year at 17-20 cm. In the Northwest Atlantic, the corresponding average, M_{50} occurs at age 12-14 (35-45 cm). Flemish Cap females matured much younger than those from other areas (7.76 years) and they also have the fastest initial growth rate (Fig. 14) probably because of the higher water temperatures. Alm (1959) indicated that fast early growth resulted in earlier development and maturation of the gonads, possibly because of earlier production of the appropriate hormones by the pituitary gland. The relation of sexual maturity to changes in growth will be discussed in Section 3.

Fecundity

Fecundity of Grand Bank and St. Mary's Bay plaice was found to be directly related to length and weight. Age-fecundity gave a very wide scatter of points and was not particularly useful unless related to the size at age.

A comparison between rate of egg production (regression coefficients) for plaice of the European and North American forms indicates a remarkable similarity as indicated in Table 8.

As indicated elsewhere, the European form matures at a much smaller size (down to 15 cm) and at a younger age (2 yrs) than plaice in the Northwest Atlantic.

From the available data there was no indication of significant differences between egg production of plaice at comparable size from different localities although there were considerable differences in the size at comparable age.

Growth for different geographic regions

Growth of fish depends ultimately on the availability

Table 8. Comparison of the regression coefficients for fecundity relationships of the North American and European forms of Hippoglossoides platessoides.

Log fecundity related to	North American form	European form
Log length (cm)	3.1709	3.5533[a] and 3.0621[b]
Log weight (g)	0.9011	1.1388[a] and 0.9461[b]
Log age (years)	1.1781	1.0033[a] and 1.0328[b]
Log av. wt. (g)	0.6848	0.6907[a] and 0.8117[b]

[a]February 1954 samples.

[b]March 1954 samples.

(European date from Bagenal 1957a)

and utilization of food with growth occurring when more food is obtained and digested than is required for maintenance (Brown 1957). Temperatures apparently control the utilization of food by the fish so that outside these temperature limits no growth occurs regardless of the food supply. Other environmental factors may have some influence on the growth of fish but only temperature and the availability of food have been investigated to any great extent for most marine species.

In relating the environment to growth, there is always the possibility that fish frequently change their habitat. Plaice on the eastern slope of the Grand Bank possibly make seasonal migrations between deep and shallow water, thus changing their environmental temperature from -0.5° to 2°C. However, positive correlations were found between lengths at ages 5 and 15 years and average bottom temperatures (Fig. 15).

The Flemish Cap and southwest Grand Bank populations are among the fastest growing fish for the whole Northwest Atlantic range of this species and St. Mary's Bay stock the slowest (Fig. 24). Other localities have been included here to fill in most of the geographic range of this species using female fish only.

The Clyde population of the European form of *Hippoglossoides platessoides* has a rapid initial period with a comparatively short life span (Bagenal 1957). Cap Cod plaice also has a rapid rate of growth in the initial year with very few fish living beyond age 10 (Lux 1970).

The apparent effects of changing population size on the growth of plaice on the Grand Bank will be discussed in Section 3.

Food and feeding

American plaice are normally caught at or near the bottom of the sea, but there is evidence that they also assume limited pelagic habitats and move to shallower water layers at night (Beamish 1966; and Pitt 1967a). Stomachs of Grand Bank plaice, while they contained such benthic forms as echinoderms and pelecypods also contained pelagic forms: euphausiids, amphipods and capelin. Sand lance (Ammodytes), a major food item, are known to make vertical diurnal movements although they usually inhabit the benthic region.

The importance of fish as a food for this species is clearly demonstrated. De Groot (1969 and 1971) predicted that Hippoglossoides platessoides should be a fish feeder because of the structure of the alimentary canal, gill rakers and eye size although most of the specimens that he examined were feeding on invertebrates. Most references to food of adult American plaice by Hunstman (1918) and

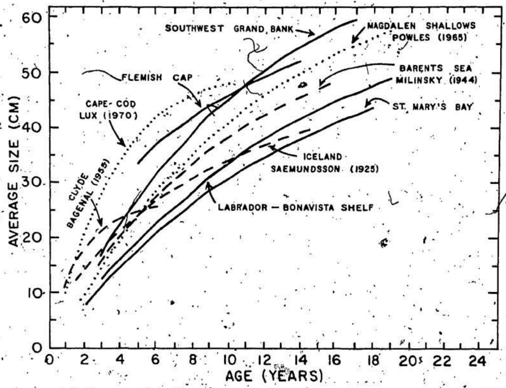

Fig. 24. Age-length relationships for female plaice, Hippoglossoides platessoides, for different areas of the geographic range.

Powles (1965) for the Gulf of St. Lawrence and Bigelow and Schroeder (1953) for the Gulf of Maine listed echinoderms, crustaceans and molluscs as the principal diet and Yanulov's (1962) brief reference to Division 3L plaice food and feeding gave echinoderms, polychaetes, and pelecypods as the major food items. However, the evidence presented here indicates that fish comprised 50-83% of the total weight of food. In the Barents Sea, Komarova (1939) indicated that while benthic forms were important as food for this species, fish, primarily cod and capelin and haddock, were also of importance.

The fact that capelin and launce occurred in a significantly greater proportion of the stomachs in Division 3N (29.6%) than to the north (Div. 3L) (9.1%) was probably just a function of the size of the habitat and the relative availability of the prey species. On the southeastern portion of the bank (Division 3N) both the predator and prey beyond the 50-fath (91-m) contour, are concentrated on a relatively steep slope and are presented with rather narrow temperature zones, whereas to the north in Division 3L with a larger area and a very gradual slope the probability of an encounter between the predator and prey was much less. The same perhaps applied to pelagic or semi-pelagic crustaceans which occurred most frequently in the southern samples. The special importance of echinoderms in Division 3L was evident; they accounted for about 30% of the total weight of food there as compared to less than 10% in Division 3N. Other evidence of greater dependence on benthic forms in Division 3L was the more frequent occurrence, and a larger percentage of the total weight of pelecypods and polychaetes.

The difference in caloric value of stomach contents for the two areas (Divs. 3L and 3N) (Fig. 23) largely reflects differences in the amounts of fish consumed. In Division 3L plaice stomachs contained fish but not in such large numbers as in Division 3N and total weights for fish were higher in the latter area.

An interesting possibility is that the greater consumption of high energy food in Division 3N as opposed to 3L produced the observed faster growing and earlier maturing (Pitt 1966) fish there. Good correlations were shown between the size at age 5 and 15 and the probable bottom temperature with faster growth in Division 3N being related to higher average temperature than in Division 3L. McKenzie (1934 and 1935) and Kohler (1964) suggested that, for cod, temperature was related indirectly to growth inasmuch as it controlled food consumption. MacKinnon (1972b), however, found no significant difference between the standard metabolic rates of American plaice at temperatures 1° and 6°C. Low temperatures may however reduce the feeding rate because of a reduction in the rate of digestion. Rae (1965), for the lemon sole (Microstomus kitt), concluded that the quantity and the type of available food was the major reason for the difference between areas in the rate of growth, and Martin (1952) found that fish-feeding lake trout in Algonquin Park, Ontario, matured earlier and grew faster than the plankton feeders. However, further speculation on the relationship between food and growth is beyond the scope of this paper.

SECTION II POPULATION ASSESSMENT

Introduction

In this section an assessment of American plaice in ICNAF Divisions 3L and 3N will be presented using primarily a model that has been widely accepted in fisheries management.

In managing a commercially exploited fish stock, one needs to know how many fish can be removed annually and still allow the stock to maintain itself at a level where the production of recruits and growth are maximized.

The fishery for plaice on the Grand Bank has been in progress since the late 1940's but it was only in fairly recent years that it has become of major importance and in 1973 it came under international quota regulation.

Methods

In recent years methods have been developed permitting the calculation of stock size from the annual numbers removed. The basic data requirements are complete records of all fish caught in the study area and sufficient fish sampled and aged to allow for the estimation of total numbers caught at each age.

Nominal Catches

The compilation of total nominal catch was complicated because certain European countries up to 1972 reported their total landings of plaice, yellow-tail flounder (Limanada ferruginea) and witch (Glyptocephalus cynoglossus) as "unspecified flatfish". However, the ICNAF Secretariat in 1974 received a breakdown of the catches of the various flatfish by European countries for 1963-72 (Anon 1974). For the pre-1963 period the separation of species was based on the proportions of these in Canadian landings.

An important omission in these data was the amounts of plaice discarded by certain countries that were fishing only for cod. The discarded fish are probably all dead. Thus is is possible that Spanish pair trawlers caught quantities of flatfish that never appeared in official statistics. In the assessments made here and for all of the estimates of stock size used for the correlations with growth (Section 3) only reported nominal catches of plaice were used. However, as a separate exercise the possible effect of non-reported by-catches and/or discards on estimates of stock size and Total Allowable Catch was computed.

Calculation of numbers caught

Estimates of numbers caught at each age were based on samples from the Newfoundland commercial fleet. Up to the late 1960's, random length measurements were taken from commercial landings during 2-week periods, normally on a quarterly basis, and fish selected for otolith sampling. More recently, stratified samples were taken from each 2-cm group based on a method described by Gulland (1955). Since both random and stratified samples were adjusted to the measured frequency, both methods gave comparable results; however, the stratified method gives better representation at the smaller and larger length groups.

The mechanics of estimating numbers measured at each 2-cm length group were adjusted to the total catch of the sampled boat by the ratio of the weights of the sampled boat and the sampled fish and then to the total numbers caught (quarterly or semi-annually) at each length by the ratio of weight landed (total) and the weight of all sampled boats. In all cases the catch and landings were broken down by sex from the proportional weight of sampled fish. Finally, age-length keys were applied to the length frequency of total numbers at length to give the number caught at age.

When sufficient data were available, age-length keys were compiled for January-June and July-December to take care of possible growth during the year that could bias the results when adjusting to measured frequencies.

Estimates of fishing effort and catch per unit effort

Information was obtained from fishing logs recorded on board most trawlers operating from Newfoundland ports. The Newfoundland-based trawlers catch a major proportion of the total plaice landings from the Grand Bank so that these log records are probably representative of the whole plaice fishery for this area.

The basic unit of fishing effort was the number of hours fished by Canadian stern otter trawlers 501-900 tons (ICNAF tonnage Class 5). Up to 1964-65 the Canadian fleet was composed almost entirely of side trawlers 151-500 tons (ICNAF tonnage Class 4). Since then, however, stern trawlers were phased in fairly rapidly so that by 1972 most of the fleet consisted of this type.

To convert earlier side trawler information to standard stern trawler equivalents, monthly catch per hour by Newfoundland side trawlers (Class 4) for individual unit areas were plotted against comparable data for stern trawlers (Class 5). The slope of the line of best fit drawn by eye, passing through the origin had a slope of 0.8 and the latter was used to convert Class 4 effort to Class 5.

Catch per hour was compiled in two ways (a) "main species plaice" from catch and effort data where plaice was taken in the largest quantities in relation to other species making up the catch from a particular trip from a single statistical area (directed fishery) and (b) "plaice recorded in catch" which uses all catches and effort where any quantity of plaice was caught.

Standardization of the U.S.S.R. and other European landings by large factory trawlers (ICNAF tonnage Class 6 and 7) presented difficulties since insufficient data were available to make comparison with Canadian catches. Total effort for ICNAF Divisions 3N and 3L was therefore estimated by dividing total reported catch of all countries by catch per hour by Canadian class 5 trawlers.

$$\text{i.e.} = \frac{\text{Total catch (All countries)}}{\text{Catch per hour Canadian class 5 otter trawlers}}$$

Calculation of possible discards and numbers caught by non-reporting countries

The only real information available from non-reporting countries was catch and effort for cod from pair and regular otter trawlers. Based on this information, assumptions were made to give estimates of discards. Data from Divisions 3L and 3N were combined for these calculations.

Method 1 used the cod catches of Spain, Portugal and France (M)* by pair otter trawler and assumes that the total catches from these gears were made up of a certain proportion of flatfish with the total catch of cod and flatfish estimated from the amount of cod reported. In this way, possible discards were estimated and added to

* metropolotitan

the reported nominal catch to give total plaice and yellowtail flounder catches. Since proportion of flatfish in the total catch (cod and flatfish) was probably not the same for all ICNAF Divisions and in order to be as realistic as possible, discards for each Division were estimated separately. Thus in Figure 35, 30%, 50%, 50% refer to percentage of plaice of total catch in Divisions 3L, 3N and 3O, respectively.

Method 2 used effort data by the same countries and gears with Spanish otter trawler hour as a standard unit of effort, i.e. catch per hour of Spanish otter trawlers was divided into total catch of Spain, Portugal and France (M) to determine total standard hours for each year. This effort was converted into American plaice catches using Canada (N) catch per hour and assuming these countries caught plaice (a) at the same rate as the Canadian trawlers (100%), (b) at 50% and (c) at 10%. These estimated catches were added to known nominal catches (Fig. 36).

New estimates of numbers caught at age (C_t^{1}) were estimated by multiplying the calculated numbers used in previous assessments of these stocks by the ratio of the new catch estimates to the previously recorded landings, i.e.

$$_{n}C^{1}_{t} = {_{n}C_{t}} \frac{(W_2)}{(W_1)}$$

Where $_{n}C^{1}_{t}$ = new estimates of number caught at age t in year n, $_{n}C_{t}$ the previous estimates of this value, W_1 the reported nominal catch for year n, and W_2 the estimated catch by methods 1 or 2.

This method was considered justified since length frequencies from Spanish pair trawlers in the previously-mentioned commercial experiment in 1974 were similar to those from the Canadian trawler fishery for the same period. (Unpub. report by the St. John's Biological Station).

The various estimates of catch at age were applied to Pope's (1972) Cohort Model (Appendix 1) and population sizes for the various simulations calculated. From those, Total Allowable Catches were estimated. These calculations were thus simmulations of what could have taken place in the fishery if the non reported catches were as great as the estimates given.

Calculation of fishing mortality (F) and stock size

The basis of the method used in estimating fishing mortality and stock size is the Baranov (1918) catch equation

$$C_n = \frac{F_n}{Z_n}(1-e^{-Z_n})N_n$$

where C_n = number of fish caught in year n, N_n = numbers present in the population at the beginning of the year and F_n and Z_n respectively fishing and total mortality during year n.

The recent use of this method in fisheries assessments for which W.E. Ricker (Personal communication) has suggested the title "sequential computation of the rate of fishing and stock size" developed from the virtual population method first introduced by Derzhaven (1922) and later by Fry (1949 and 1957) and again further modified by Gulland (1965). By this method (Gulland's modification) year-classes that have passed completely through the fishery can be used to calculate fishing mortality and stock size. Details of this method are given by Schumacher (1970). The calculations are based on the summations of the contribution that each age group makes to a year-class. Thus the number of fish of the year-class x which are caught in year n or later is given by

$$ {}_xV_n = {}_xC_n + {}_xC_{n+1} \text{ .... etc.} $$

(where ${}_xC_n$ = catch of fish of x year-class in year n)

Thus survival of x year-class in year n is given by

$$ \frac{{}_xV_{n+1}}{{}_xV_n} $$

However, since this method uses only year-classes that have passed completely through the fishery, it obviously precludes the use of data from recent year-classes which contains incompletely exploited year-classes, and since in the case of American plaice on the Grand Bank the most recent years were the periods of greatest fishing activity, it would be desirable hence to bring estimates of stock size up to date as far as possible.

Jones (1961 and 1968) described a method that allowed the calculation of F and stock size when a year-class had not completely passed through the fishery and could thus provide current F values. His starting point was the ratio

$\frac{C_{n+1}}{C_n}$ where C_n and C_{n+1} are the catch of a particular year-class in year n and n+1 respectively. His method is also described in detail by Schumacher (1970).

More recently a further modification of these methods was developed by Pope (1972) based on estimates of population sizes of a cohort of fish at successive age intervals from which estimates of total mortality can be derived and by subtracting M (Natural Mortality) values of F can be obtained for each age group. Details of this Method, "Pope's Cohort Analysis", is described in detail in Appendix No. 1. This method was used in the assessment presented here.

For each method and for all population models it is necessary of course to have an estimate of natural mortality (M).

In presenting data on stock size only fully recruited age groups were presented. Thus in Division 3L males are fully recruited to the fishery at age 12 and females at 15 whereas in 3N the corresponding ages are 10, and 13 years. However, since the numbers presented are males and females combined, very few males would be included in totals starting at the age of full recruitment of the females, hence in addition to the age 15 fish and older, 13 and 14 year olds were also included for Division 3L and 11 and 12 year olds for Division 3N.

Obviously the accuracy of fishing mortality and stock size is dependent on estimates of numbers caught and as pointed out previously, because of the lack of data on discards, catch estimates are probably minimal and thus probably also the estimates of stock size.

The prediction of stock and catches (Tables 10 and 11 was accomplished by using the Baranov catch equation with known or estimated values of two of N (Stock numbers), catch numbers, or F

$$\text{i.e.}\quad C_n = N_n \frac{F_n}{Z_n}(1-e^{-Z_n})$$

$$N_n = \frac{C}{\frac{F_n}{Z_n}(1-e^{-Z_n})}$$

$$\frac{F_n}{Z_n}(1-e^{-Z_n}) = \frac{C}{N_n}$$

$$\text{and } N_{n+1} = N_n e^{-Z_n}$$

The 1973 population and catch estimates (numbers) were used to calculate F values for 1973 and the population at the beginning of 1974 (Tables 10 and 11). Then using the latter and the 1974 catch, a projection for 1975 population was made with F values at $F_{0.1}$ (see pages 97 & 98) and partial recruitment values, catches for 1975 were calculated. Average recruitment at the youngest recruitment age was assumed and the process repeated to give catches for 1976. To get weight, numbers at age were simply multiplied by corresponding mean weights for the most recent data.

Estimation of natural mortality of American plaice, (Huntsman 1918 and Powles 1969)

Huntsman (1918) estimated that the total mortality rate for males and females combined, from an unexploited population of plaice from the southern part of the Gulf of St. Lawrence was 12.5% per annum ($Z = 0.14$). Huntsman's data used to fit a catch curve gave an M of 0.21 for ages 9-22 and 0.18 for ages 9-24 (Fig. 25A). Powles (1969) from a sample collected in 1950 just at the beginning of the otter trawler fishery for this species estimated Z at 0.13 using the

Jackson (1939) method of average survival, i.e.

$$S. = \frac{N_{10} + N_{11} \cdot \cdot \cdot \cdot \cdot \cdot \cdot N_{19}}{N_{9} + N_{10} \cdot \cdot \cdot \cdot \cdot \cdot \cdot N_{18}}$$

where N = number of fish of an age group in the sample. However, using Robson and Chapman's (1961) modification gave a value for Z of 0.26 ± 0.092.

Fitting a straight line to these data (i.e. the catch curve method) for fish, age 10 to 19 gave a Z value of 0.29 and 0.26 for ages 9-19 (Fig. 29A). Powles (1969) calculated fishing and natural mortality coefficients for plaice tagged in the Magdalen Shallows of the Gulf of St. Lawrence using a method developed by Paloheimo (1958) calculated M at 0.11 to 0.16 (sexes combined). This method is apparently subject to considerable error since it involves estimations of fishing mortality coefficients (F) from tagging returns from assumed values of M and an independent estimate of Z from catch curves.

Male plaice normally have a shorter lifespan than females. Males as previously indicated also become sexually mature at an earlier age. These facts suggest that natural mortality was probably different for the sexes, hence independent calculations were made.

Natural morality coefficient estimates from age composition of unexploited populations of plaice

The relatively small population of plaice in

St. Mary's Bay was not exploited commercially until the mid-1960's. Tagging data (Pitt 1969) (and Section 1) indicated that this population is discrete and hence not affected by exploitation on the Grand Bank (Fig. 25B).

Hamilton Inlet Bank (ICNAF Division 2J) also supports a small plaice population that is probably also discrete from the Grand Bank. This area is at present heavily exploited primarily for cod and since plaice sometimes frequent the same habitats as cod, some plaice were removed by fishing. However, prior to 1960 fishing intensity in this area was much less than in recent years, resulting in less than an average yield of 40,000 tons of cod annually for 1954-60 as compared to 260 thousand tons in 1960 and 280 thousand tons in 1961 (May 1967). Thus, for 1957-59 removal of plaice incidental to cod catches was probably minimal.

Age composition of research samples from St. Mary's Bay 1957-60 and Hamilton Inlet Bank 1957-59 were hence used to calculate natural mortality coefficients on the assumption that for these populations Z = M. A straight line fitted to the descending limbs of the catch curves (Fig. 25B and C) give estimates of M as follows:

St. Mary's Bay	Males	= 0.24
	Females	= 0.18
Hamilton Inlet Bank	Males	= 0.30
	Females	= 0.22

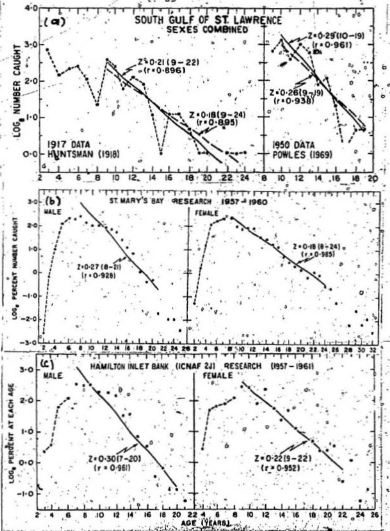

Fig. 25. Total mortality estimates from unexploited stocks for: (A) Gulf of St. Lawrence (Huntsman 1918 and Powles 1969), (B) St. Mary's Bay, Nfld., (C) ICNAF Division 2J. (Hamilton Inlet Bank)

For the latter area the possibility exists that there was some fishing mortality, but it is difficult to see that this would be more than 5% (F = 0.05) at the most.

Estimation of natural mortality from catch and effort data

Effort changing over a period of time - The use of catch and effort data to estimate natural mortality is based on the premise that catches of fish at various ages depend on abundance of fish at that age and on effort expended. The data required are numbers of fish caught for a series of year-classes over a period of years during the exploited phase and effort expended by the fleet to catch fish of the year-classes.

Beverton and Holt (1957) gave a method of calculating natural mortality where the effort was changing over a period of time. Thus fishing mortality (F) is proportional to the amount of effort expended, i.e.

$$F_n = q f_n$$

where q is the "constant of catchability" or the fraction of fish taken by a unit of effort and f_n is the effort expended in year n.

It follows thus that for any year

$$Z = qf + M$$

It would, therefore, appear that a series of values for the total mortality coefficient (Z) calculated for different levels of effort (f) would give a linear relationship having an intercept of M and a slope of q. Now basically the calculation to Z depends on the catches and effort for age group (or groups) of a series of year-classes, i.e.

$$Z = \text{Log}_e \left[\frac{{}_xC_{n+1}/f_{n+1}}{{}_xC_n/f_n} \right]$$

where ${}_xC_n$ = catch in numbers during year n of fish of the year-class born in year X and f_n the total effort in year n.

If the fishery and hence the sampling occurs at one particular period of the year, only then can Z be plotted directly against f_n.

$$\text{i.e.} \quad \text{Log}_e \left[\frac{{}_xC_{n+1}/f_{n+1}}{{}_xC_n/f_n} \right] = q\ f_n + M$$

However, this is rarely the case and for most fisheries the fishing is spread over the whole year and the survival rate is not a simple function of the survival

$$\left[\frac{C_{n+1}/f_{n+1}}{C_{cn}/f_n} \right]$$

in either year n or n+1, but in fact is related to average abundance in year n and n+1. Hence a correction factor has to be applied to account for the fact that survival rates are usually based on average, annual indicies of abundance. To take the correction into account an iterative procedure must be applied. This procedure is described in detail by Ricker (1958) and was followed here.

Paloheimo (1961) showed that instead of the long iterative method of Beverton and Holt the original values of Z could be fitted to values of f which are in fact average values of f_n and f_{n+1}, i.e.

$$Z = q \tfrac{1}{2}(f_n + f_{n+1}) + M$$

This in effect relates survival between years n and n+1 to the mean effort in the two years, or in effect, from the mid-point of year n to the middle of year n+1; assuming of course that effort is spread fairly evenly throughout the two years. When compared to the Beverton and Holt method Paloheimo found that his method gave virtually the same values of M.

Using both the Beverton and Holt's and Paloheimo's methods applied to 14-, 15- and 16-year-olds for males and 17-, 18- and 19-year-olds for females gave the results indicated in Fig. 26. Except for the 3N males, significant correlations were obtained. Because of the wide scatter of Z in relation to f_n and $\tfrac{1}{2}(f_n + f_{n+1})$ the errors of the estimate were relatively large. This is apparently usual for estimates made by these methods (Ricker 1958; Paloheimo 1961). The reason for the poor fit for 3N males is the high values of Z for low effort levels. The only explanation that can be given for this is the possibility of errors in the original age-length keys which were sometimes based on relatively small samples. Editing of the data by elimination of high values of Z gave a better correlation and M values of 0.17 and 0.22 for Beverton and Holt's and Paloheimo's methods respectively.

As a further estimate of natural mortality coefficients, unweighted estimates of Z were calculated from catch curves for a series of year-classes (Fig. 27) and plotted against the mean of the effective effort as calculated by the Paloheimo method (Fig. 28). These showed fairly close agreement with estimates by the two previous methods. Again, high estimates of Z from relatively low levels of effort for 3N males produced a high value for M. Since estimates of Z from catch curves are really average values, there was less variation and hence lower values for the standard error of the estimate of M.

Calculation of yield per recruit

The relationship between average yield and the amount of fishing (fishing effort, or fishing mortality) is usually expressed on yield-per-recruit curves (Fig. 29). Yields-per-recruit were calculated separately for males

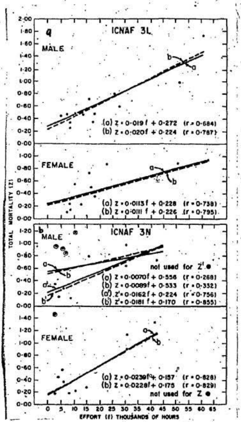

Fig. 26. Estimates of M by (a) Beverton and Holt's (1957) interative method and (b) Paloheimo's (1961) linear formulae.

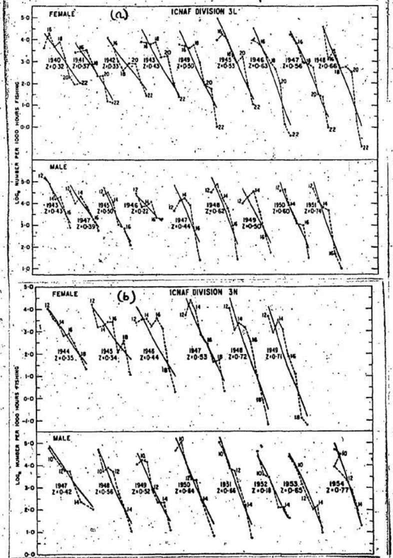

Fig. 27. Catch curves of plaice (a) from Division 3L, 1940-48 year-classes for females and 1943-51 for males (b) for Division 3N, 1944-49 year-classes for females and 1947-54 for males. Lines fitted 12-19 (female), 9-15 (male).

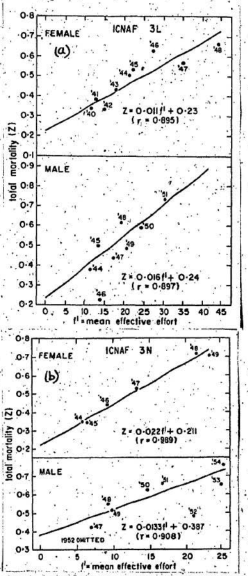

Fig. 28. Estimate of M (a) in Division 3L and (b) in Division 3N using Z from catch curves from Fig. 27.

and females on the basis of a million recruits annually at age 3.

During the pre-recruited phase, fish are subjected to natural mortality (M) only but as recruitment to the fishery occurs they are subjected to an increasing rate of fishing mortality in addition to natural mortality. Points on the yield-per-recruit curve are calculated by summing the weight contributed to the catch by each age group during the exploited phase at suitable intervals of F on the axis of the yield-per-recruit curve, i.e.

$$\text{Yield in weight } (Y_w) = \sum_{i=3}^{n} \overline{W}_i \left[N_i \frac{P_i F}{P_i F + M} \left(1 - e^{-(P_i F + M)} \right) \right]$$

where $\overline{W}_i$ = mean weight at age, N_i = stock size (numbers) at the beginning of the year, i = age, n = life span, P_i = partial recruitment (%) at age i, and F and M fishing and natural mortality.

The yield curves (Fig. 29) are essentially flat-topped without an obvious maximum yield-per-recruit point (F_{max}). Hence the $F_{0.1}$ level was selected as the point on the curve where the fishery should be in terms of fishing mortality or effort. Gulland and Boerema (1972) define $F_{0.1}$ as the marginal yield, i.e. the increased yield per recruit produced by adding one unit of effort is one-tenth of the yield produced by the first unit of effort introduced to the unexploited fishery $F_{0.1}$

is thus somewhat arbitrary and is intended as a reference point at which to regulate the fishery. The sustainable yield per recruit on the average reaches approximately 90% of the MSY on a "flat-topped" curve.

The calculation of $F_{0.1}$ is by graphic means as indicated for Division 3L males in Fig. 29. A tangent ab is drawn to the curve at the origin and at levels of F yield-per-recruit point are selected on ab and a line, ac, drawn to pass through points which are 10% of those selected on ab. The $F_{0.1}$ is determined by a tangent to the curve parallel to ac.

RESULTS

Trends in nominal catch, 1955-73

In Division 3L annual landings increased very gradually from 1955 to 1966, at a level just below 20,000 tons. In 1967, landings increased sharply, reaching a peak of approximately 52,000 tons in 1969 then declined to about 20,000 tons in 1973 (Fig. 30). In Division 3N catches in early years were around 5,000 tons, increased sharply in 1964, peaked at about 35,000 tons in 1966, then declined to around 15,000 tons in 1969. Since then, catches have averaged about

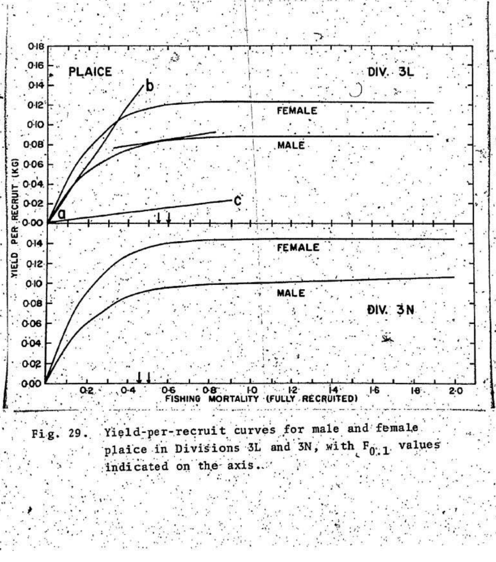

Fig. 29. Yield-per-recruit curves for male and female plaice in Divisions 3L and 3N, with $F_{0.1}$ values indicated on the axis.

15,000 tons annually. On the southwest part of the Grand Bank (Division 3O) except for large reported catches by the European fleet in 1966-69, as mentioned earlier, catches have remained generally below 10,000 tons.

The increase in plaice landings during the early and mid-1960's can be easily explained. Up to 1961-62, the haddock fishery was very important to Canadian and foreign fishing fleets. As haddock stocks declined and fishing by Newfoundland-based component of the Canadian fleet expanded, effort was directed to plaice first in Division 3N and later in Division 3L. The European fleet, mainly U.S.S.R., fished primarily in Divisions 3N and 3O with much of the catch of plaice being a by-catch probably in the fishery directed to catching cod. There is no indication that the increase in landings was because of improved availability of plaice.

Fishing mortality (F) for fully recruited plaice

Estimates of F at corresponding ages were generally higher for males than females (Table 9). Although males were usually smaller at comparable ages, they apparently became vulnerable to capture earlier, since length frequencies for both research and commercial catches indicated a preponderance of males at lower size groups (Pitt 1973). The reason for this is not apparent, but

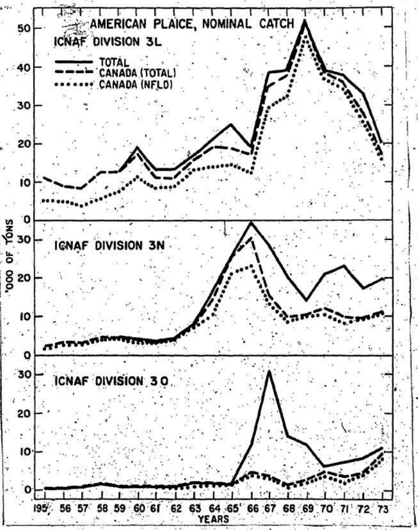

Fig. 30. Nominal catches of plaice from Divisions 3L, 3N and 3O.

the 50% maturity point for males is age 6 (about 24 cm) in Division 3L and age 5 (about 26 cm) in Division 3N, whereas for females it is 14 years (40 cm) and 9 years (41 cm) in Divisions 3L and 3N respectively. Just how early maturation of males could result in earlier vulnerability is not clear. Males are fully recruited at age 11 in Division 3L and age 9 in Division 3N whereas for females the corresponding ages are 15 and 13 years. (Pitt 1973).

Values of F in Division 3L were generally 0.15-0.25 for both males and females up to the early 1960's. (Table 9) For males the rate increased after 1961 to 1.18 in 1969 and 1.06 in 1970, however, these could be aberrant since they were calculated from data producing values for ages 12 and 13 only, however F increased to 1.2 in 1972 and was 1.05 in 1973. For females average values of F were generally lower up to 1971 but reached maximum values of 1.26 and 1.28 in 1972 and 1973.

In Division 3N there was no real increase in F for males until 1966 when a value of 0.48 was calculated and the highest value 1.39 was calculated for 1973 (Table 9). For females, F increased gradually from 0.10 in 1956 to 0.30 in 1965 with an overall upward trend giving a peak value of 0.78 in 1973.

Table 9: List of catches, total effort, catch per unit effort, and average instantaneous fishing mortality (F) for plaice from ICNAF Divisions 3L and 3N. Values of F are for fully recruited fish for the ages shown.

Year	Division 3L							Division 3N						
	Nominal catch (tons)	Effort (thous. hr)	Catch per hr (kg)*	Male F	Male Ages	Female F	Female Ages	Nominal catch (tons)	Effort (thous. hr)	Catch per hr (kg)	Male F	Male Ages	Female F	Female Ages
1955	11,518	7.3	1578	0.15	12-16	0.14	15-20	2,193	2.3	950				
1956	9,125	8.4	1083	0.16	12-16	0.19	15-20	3,162	3.3	952	0.12	10-14	0.10	13-18
1957	8,466	8.7	977	0.11	12-16	0.25	15-20	3,198	3.9	815	0.18	10-14	0.14	13-18
1958	12,745	10.7	1190	0.21	12-16	0.25	15-20	4,550	8.6	530	0.27	10-14	0.15	13-18
1959	12,656	13.5	940	0.29	12-16	0.27	15-20	4,506	6.0	749	0.30	10-14	0.17	13-18
1960	19,379	18.8	1030	0.25	12-16	0.23	15-20	3,912	5.1	774	0.30	10-14	0.15	13-18
1961	13,398	14.6	918	0.25	12-16	0.26	15-20	3,448	5.5	624	0.19	10-14	0.18	13-18
1962	13,584	16.9	802	0.31	12-16	0.30	15-20	3,923	7.9	499	0.19	10-14	0.18	13-18
1963	16,516	18.7	901	0.45	12-16	0.27	15-20	7,465	10.4	719	0.29	10-14	0.24	13-18
1964	20,909	26.4	792	0.47	12-15	0.26	15-20	14,587	15.1	964	0.25	10-14	0.24	13-18
1965	25,034	29.2	864	0.42	12-15	0.32	15-20	26,270	31.0	846	0.31	10-14	0.30	13-18
1966	18,572	25.2	737	0.47	12-14	0.31	15-20	34,698	41.8	829	0.48	10-14	0.37	13-18
1967	38,515	54.3	710	0.53	12-14	0.42	15-20	24,364	30.1	810	0.54	10-14	0.45	13-18
1968	39,726	68.8	568	0.83	12-14	0.47	15-19	20,038	35.2	570	0.69	10-13	0.45	13-17
1969	52,880	100.1	527	1.18	12-13	0.50	15-19	14,442	31.5	459	0.48	10-11	0.35	13-18
1970	39,347	87.4	449	1.06	12-13	0.55	15-20	21,032	61.9	340	0.56	10-11	0.52	13-18
1971	37,851	88.0	430	0.67	12-14	0.64	15-20	22,873	81.2	282	0.48	10-12	0.55	14-18
1972	33,330	74.1	447	1.20	11-14	1.26	15-19	17,387	58.0	300	0.40	11-13	0.46	14-19
1973	20,103	41.6	483	1.05	11-14	1.28	15-19	20,883	64.6	323	1.39	11-13	0.78	14-19
1974	16,609	41.3	402	-	-	-	-	21,118	75.9	278	-	-	-	-

*Plaice recorded in catch.

9	.13	39.7	39.0	50.0	37.2	.43	11.3	10.4
10	.19	24.8	30.1	30.1	37.6	.66	6.3	6.9

Catch per unit effort

A downward trend in catch per hour for both weight (Fig. 31A, Table 9) and numbers caught (Fig. 31B) was evident in Division 3L. Weight landed per hour declined from 1578 kg (plaice in catch) in 1955 to approximately 430 kg in 1971 and 1972 with a similar trend when plaice was the main species sought. For numbers caught per hour the trend is similar but slightly more irregular. The increase in numbers per hour for 1971-73 can be attributed, in part at least, to the fact that more small fish were landed by the Canadian fleet than in previous years.

In Division 3N the trend up to 1964 is not clear, but from 1956 to 1962 there was an overall decline in the catch per hour (weight) (Fig. 31A, Table 9). The catch per hour increased from 700 kg in 1962 to 1050 kg in 1964 (plaice main species) followed by a general downward trend. For numbers caught per hour the pattern is similar except that the 1960 peak is more pronounced (Fig. 31B). As a further index of abundance the numbers caught of the older age groups were also presented (Fig. 31B). For both divisions a general downward trend is evident.

Stock size

An overall decline in stock abundance of fully recruited plaice (15 years and older) and at a slightly younger age (13 years and older or 75-80% recruited) was evident in Division 3L (Fig. 32) for the period 1955-73. In Division 3N, however, the fully recruited stock appeared to decline from 1956 to 1962 then increase to reach a peak in 1965 and 1966, followed by a downward trend to 1972 with an upward trend again in 1973. With slightly younger fish included (11 years and older, 75-80% recruited), the stock appeared to increase in abundance from 1959 and reached a peak in 1966, followed by a decline to 1972 and an increase in 1973.

Relating catch per unit effort to abundance

Since estimates of numbers present in the stock are most reliable for age groups that are completely or nearly completely vulnerable to the gear, only these estimates were used here.

For Division 3L straight line relations can be demonstrated with highly significant correlation coefficients ($P < 0.001$) for weight caught per unit effort, and numbers caught per unit effort (Fig. 33A and B) for the fully recruited (15 years and older) and for the stock (13 years and older). In Division 3N (Fig. 33A and B), although a significant correlation was found between stock size of fully recruited ages (13 and older) and weight caught per unit effort ($P = 0.04$),

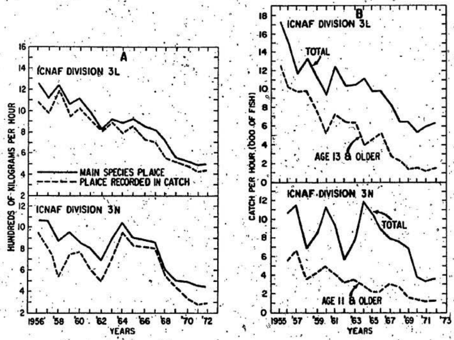

Fig. 31. (A) Catch per hour (kg) of Newfoundland-based trawlers for Divisions 3L and 3N. (B) Catch per hour (number) for total catch and for fish 13 years and older and 11 years and older in Divisions 3L and 3N respectively.

no significant correlation could be demonstrated for the plot of fully recruited stock size on numbers caught per hour (P = 0.06). For the younger age group (11 and older) correlation coefficients were not significant for either relation (P = 0.5 and 0.8 respectively). However, using just the data for 1962-72 did give significant correlation for both the weight caught per hour (P = 0.02) and for numbers per hour (P = 0.04).

These correlations seem to support the validity of the effort data used in calculating the catch per unit effort.

Relating fishing mortality (F) to effort

The regression of average values of F for fully recruited age groups on effort gave highly significant correltions for the 1955-72 data (Fig. 34). Since only one type of gear was used to fish plaice and since they probably do not have marked seasonal distribution patterns, it was felt that the calculation of effort was probably a good measure of fishing intensity (catch per hour per unit area). The values of F calculated for the early years appears to be too high in relation to the effort since obviously the regression line should pass through the origin and thus relate to the plot in Figures 26 and 28. It was possible that F was underestimated especially in the early years and, in the light of recent

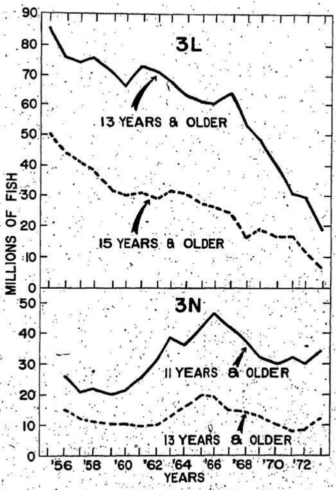

Fig. 32. Stock abundance of 12+ and 15+ year old fish in Division 3L and 10+ and 12+ fish in Division 3N.

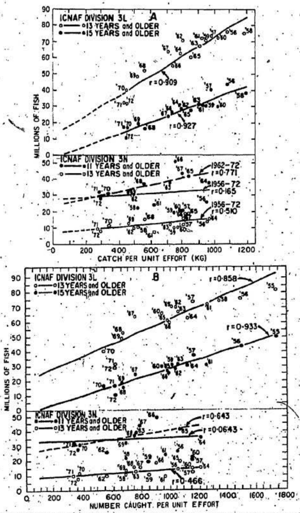

Fig. 33. (A) Relationship between catch per hour (wt) and stock abundance in Divisions 3L and 3N. (B) Relationship between catch per hour (Number) and stock abundance.

data on the European fleet not reporting plaice catches, it appears likely that effort was underestimated throughout the period. It should be emphasized however that the error of the estimate for these plots is quite large.

Another possible reason why the regression line did not pass through the origin was that M (natural mortality) was too high. Natural mortality is considered to be constant throughout the life span. This of course is probably not the case since the first year or so and in the last few years of life M is perhaps relatively high.

Except for the 1973 values for both Divisions and the higher values in Division 3L for 1972, the lines fit the data fairly well and, at least up to recent years, was considered to be a good method of determining F from a known level of fishing effort.

Stock assessment and predictions

Catches of plaice in 1973 were 20,000 tons in Division 3L and 21,000 tons in Division 3N (41,100 Divs. 3LN). In 1974 catches of 16,600 tons in Division 3L and 21,100 in 3N (37,700 tons for Divs. 3LN) were reported. The projected total allowable catch (TAC) for 1973 based on an assessment made in 1972 and utilizing data up to 1971 (Pitt 1973) was a total of 52,000 tons for both divisions combined (approximately 30,000 tons

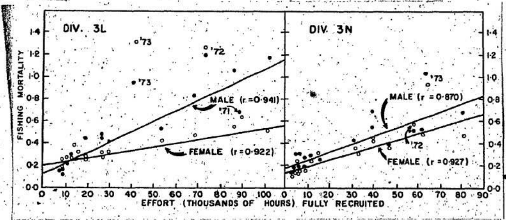

Fig. 34. Regression of mean annual fishing mortality for fully recruited age groups on fishing effort for Divisions 3L and 3N (fitted for 1955-71 data).

for Div. 3L and 22,000 tons for Div. 3N). The calculations were based on average recruitment and a fishing mortality rate for the fully exploited age groups at $F_{0.1}$ for both Divisions (3L male = 0.6 and female = 0.55; 3N male = 0.50 and female = 0.45).

Subsequent assessments made in 1973 and 1974 (Pitt 1974) using 1972 and 1973 catch data respectively projected total allowable catch (TAC) for 3LN of approximately 50,000 tons for 1974 and 46,800 tons for 1975. The latter was based on a Cohort Analysis using a final F (F_n Page 166 Appendix i) for 1973 extrapolated from Figure 34 (F on effort). This analysis or computation gave a stock size at the beginning of 1973 and estimated stock for 1974 and 1975. Then using the previously determined TAC (broken down by numbers at age) and assuming a fishing rate at $F_{0.1}$ in 1975 gave a projedted TAC for Divisions 3LN. However, when the 1974 catch data became available in the spring of 1975 and a new Cohort Analysis computed, it was found that F for 1973 was much higher than the value used in initiating the previous years analysis (Div. 3L = 1.28 and 1.05 for females and males respectively with corresponding values of 0.78 and 1.39 for Div. 3N) and hence the calculated stock sizes at the beginning of 1973 and 1974 and projected stock size for 1975 were too high.

Thus the compilations in Tables 10 and 11 indicate that the TAC predicted and allocated by ICNAF for 1975 will generate fishing mortalities of 0.67 and 0.73 for females and males in Division 3L respectively and corresponding values of 0.65 and 0.70 for Division 3N. These are somewhat higher than $F_{0.1}$. Assuming average recruitment at ages 6 or 7, approximately 36,800 tons (17,900 tons for Division 3L and 18,900 tons for 3N) can be removed from the fishery at $F_{0.1}$ in 1976.

Assuming average recruitment at the approximate values as those indicated in Tables 10 and 11 and taking those back to age 3, then using the yield-per-recruit curves in Fig. 29 at $F_{0.1}$ produces yields of approximately 45,000 - 50,000 tons annually for Divisions 3LN.

Possible effects of unreported discards of plaice on total allowable catches in Divisions 3LN

Present total allowable catches of plaice were calculated without taking into account possible discards by countries fishing and salting cod and not reporting flatfish (plaice, yellowtail or witch) catches either as discards or in their statistics of nominal catch. The possible magnitude of these discards is illustrated in Fig. 35 and 36. Spain, Portugal and France (metropolitan) almost exclusively report only cod catches on the Grand

Table 10: Population and catch numbers for 1973 and 1974 with projected values for 1975 and 1976, ICNAF Division 3L using 1974 catch data as the last reference year.

Age	Partial re-cruitment	Female Population No. x 10^{-6}				Partial re-cruitment	Male Population No. x 10^{-6}			
		1973	1974	1975	1976		1973	1974	1975	1976
6						.01	32.0	41.0	(40.0)*	(40.0)*
7	.023	78.3	62.0	(60.0)*	(60.0)*	.10	21.9	24.7	30.4	(30.9)*
8	.07	49.2	63.6	47.6	48.4	.23	15.3	16.4	18.1	22.0
9	.13	39.7	39.0	50.0	37.2	.43	11.3	10.4	11.1	12.0
10	.19	24.8	30.1	30.1	37.6	.66	6.3	6.9	6.3	6.4
11	.25	14.7	18.2	22.1	21.8	1.00	3.5	3.0	3.6	3.1
12	.38	8.7	10.0	13.0	15.4	1.25	1.9	0.9	1.3	1.4
13	.48	6.0	5.7	6.7	8.3	1.30	1.0	0.6	0.3	0.4
14	.60	2.9	3.1	3.6	4.0	1.30	0.3	0.3	0.2	0.1
15	.85	3.1	0.9	1.8	2.0	1.30	0.2	0.1	0.1	0.1
16	1.00	1.3	0.5	0.5	0.9					
17	1.18	0.4	0.2	0.3	0.2					
18	1.43	0.2	0.1	0.1	0.1					
19	1.40	0.2	0.02	0.03	0.03					
20	1.40	0.1	0.01	0.01	0.01					
TOTALS		230.0	231.4	235.8	235.9		93.6	103.2	111.4	116.5

*Average recruitment 1969-73

Age	$\overline{W}$ (kg)	Female catch No. x 10^{-3}				$\overline{W}$ (kg)	Male catch No. x 10^{-3}			
		1973	1974	1975	1976		1973	1974	1975	1976
6						.203	200	800	300	200
7	.270	600	1,700	800	700	.279	700	1,300	1,800	1,600
8	.326	1,400	2,200	1,900	1,700	.336	1,700	1,900	2,400	2,500
9	.459	2,600	1,900	3,700	2,300	.434	2,200	2,100	2,600	2,400
10	.584	2,400	2,700	3,200	3,400	.588	2,100	2,000	2,100	1,900
11	.729	2,200	2,100	3,000	2,600	.701	2,200	1,200	1,600	1,200
12	.861	1,600	1,700	2.600	2,600	.891	1,000	400	700	700
13	1.033	2,000	1,200	1,600	1,800	1.004	600	300	200	200
14	1.087	1,600	800	1,100	1,000	1.093	200	130	100	50
15	1.364	2,200	300	700	700	1.209	60	20	50	30
16	1.575	1,000	200	200	300					
17	1.807	300	80	130	90					
18	2.062	200	30	60	50					
19	2.311	200	10	20	20					
20	2.398	50	+	+	+					
TOTAL NO.		18,300	15,000	19,100	17,300		11,000	10,100	11,800	10,800
TOTAL WT (tons)		16,000	10,000	13,400	12,600		6,400	4,900	6,800	5,300
F (full recruitment)		1.28	0.50	0.67	0.55		1.05	0.65	0.73	0.60
TOTAL WT. MALE + FEMALE (tons)							20,100	16,600	20,200	17,900

Table 11: Population and catch numbers for 1973 and 1974 with projected values for 1975 and 1976, ICNAF Division 3N using 1974 catch data as the last reference year.

Age	Partial re-cruitment	Female Population No. x 10^{-6} 1973	1974	1975	1976	Partial re-cruitment	Male Population No. x 10^{-6} 1973	1974	1975	1976
6	0.02	71.7	62.3	(64.0)*	(64.0)*	0.03	50.0	36.0	(35.0)*	(35.0)*
7	0.04	57.8	59.6	48.0	51.7	0.12	38.1	38.5	27.0	(27.0)*
8	0.07	27.4	47.0	46.3	40.7	0.25	13.7	28.9	27.4	19.4
9	0.11	27.0	21.9	36.9	36.2	0.62	7.7	8.5	19.4	17.9
10	0.16	26.7	21.5	16.9	28.1	0.89	4.5	3.8	4.6	9.8
11	0.20	12.3	20.4	16.1	12.5	1.00	2.7	2.1	1.7	1.9
12	0.32	12.2	9.5	15.0	11.6	1.43	1.3	0.9	0.9	0.7
13	0.44	6.0	8.2	6.5	9.9	1.30	1.0	0.2	0.3	0.3
14	0.53	4.4	4.3	5.3	4.0	1.30	0.4	0.1	0.1	0.1
15	0.57	2.3	2.6	2.6	3.0					
16	1.00	0.9	1.1	1.6	1.5					
17	0.78	0.3	0.3	0.5	0.7					
18	1.09	0.3	0.1	0.2	0.3					
19	1.09	0.06	0.1	0.05	0.1					
20	1.00	0.02	0.01	0.05	0.02					
TOTALS		250.3	259.5	262.9	264.3		119.6	118.0	116.4	111.7

*Average recruitment 1969-73

Age	$\bar{W}$ (kg)	Female catch No. x 10^{-3} 1973	1974	1975	1976	$\bar{W}$ (kg)	Male catch No. x 10^{-3} 1973	1974	1975	1976
6	.229	100	1,500	800	500	.229	500	200	600	500
7	.349	400	1,800	1,200	800	.349	900	2,900	1,900	1,400
8	.424	500	1,600	1,900	1,200	.441	2,400	3,600	3,900	2,000
9	.543	700	1,200	2,300	1,600	.570	2,600	2,400	6,100	4,300
10	.724	1,600	1,700	1,500	1,800	.714	1,600	1,400	1,900	3,100
11	.993	600	1,900	1,800	1,000	.823	1,400	900	800	700
12	1.109	2,000	1,400	2,600	1,400	.990	1,000	400	500	300
13	1.285	1,700	1,600	1,500	1,600	1.074	900	70	200	100
14	1.514	1,100	900	1,400	800	1.166	200	20	40	40
15	1.778	900	600	700	600					
16	2.052	500	400	700	500					
17	2.400	100	110	200	200					
18	2.698	160	40	90	100					
19	2.884	50	30	20	30					
20	3.024	10	+	20	+					
TOTAL NO.		10,400	14,900	16,600	12,092		11,400	11,900	16,900	12,400
TOTAL WT. (tons)		12,000	12,900	16,900	11,700		7,400	6,200	9,700	7,200
F (full recruitment		0.78	0.50	0.65	0.45		1.39	0.58	0.70	0.50
TOTAL WT. MALE + FEMALE (tons)							20,900	21,100	26,600	18,900

Bank, although a major proportion of their fishery occurs at the same depth and location as the plaice fishery by Canadian trawlers. This being so, it would appear likely that plaice are taken as by-catches of the otter-trawler and pair-trawl fisheries. These quantities were not used in the calculation of total numbers caught and hence were not reflected in the prediction of total allowable catches (TAC).

The recalculation of the latter by the two methods described is merely illustrative and is meant to show the possible effects of underestimating removals. However, while these TAC's may not necessarily show the true conditions, they do indicate the possible magnitude of the problem since it emphasizes the probability of considerable quantities of this resource being discarded at sea. The calculated TAC's are shown below and estimates of stock size from the simulation in Fig. 37.

A. Method 1

Percent flatfish in total catch (cod and flatfish)

	3L 30%	3N 50%	3O 50%	3L 20%	3N 20%	3O 20%	3L 10%	3N 10%	3O 20%
	(tons)			(tons)			(tons)		
Plaice	110,000			80,500			71,000		

B. Method 2

	Percent of Canada (N) catch/hour plaice		
	100%	50%	20%
	(tons)	(tons)	(tons)
Plaice	112,000	88,000	70,000

TAC using reported nominal catches up to and including 1973 at $F_{0.1}$

Plaice = 58,000 tons (Includes 46,000 tons for Division 3L and 3N and 12,000 tons for Division 3O).

There is some evidence of removals of flatfish and other commercail species as by-catch in the Spanish pair-trawlers cod fishery. Lopez-Veiga and Vasquez (1974) reported on by-catches of Spanish pair-trawlers on the west coast of Greenland (ICNAF Divisions 1C and 1D), St. Pierre Bank (Subdivision 3Ps), Banquereau (Subdivision 4Vs), and on Georges Bank (Subdivision 5Ze) and indicated frequent commercial size catches of species such as wolffish, redfish and American plaice. The latter was reported as abundant in catches on Georges Bank, Banquereau, and very abundant off West Greenland.

The reality of this discard problem was further emphasized by an experiment conducted by a Newfoundland fishing company with two chartered Spanish pair trawlers and, although the effort was directed to cod, considerable

Table 12. Summary of catch composition and catch per hour (tons) by Spanish pair trawlers operated by Newfoundland fishing company and data from Canadian trawlers operating during a comparable period (June - mid-August 1974).

Div	Spanish pair trawlers							Canadian trawlers						
	Hr.	Cod		Plaice		Yellowtail		Hr	Cod		Plaice		Yellowtail	
		t/hr	%	t/hr	%	t/hr	%		t/hr	%	t/hr	%	t/hr	%
3L	335	0.162	68	0.075	32	-	0	2794	0.040	10	0.245	65	0.097	25
3N	27	0.011	6	-	0	0.186	94	2557	0.007	1	0.240	47	0.259	52
3O	700	0.128	48	0.016	6	0.123	46	1130	0.035	8	0.174	39	0.237	53

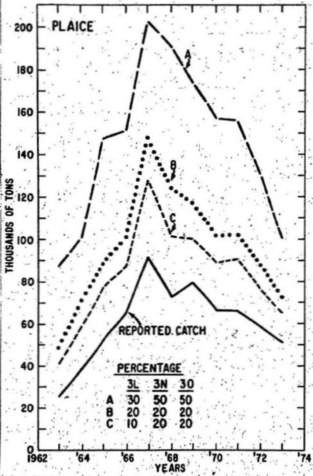

Fig. 35. Estimated catches of plaice based on landings of cod by non-reporting countries (Method I in Text).

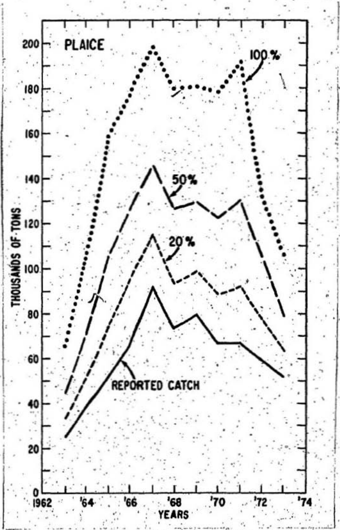

Fig. 36. Estimated catches of plaice based on effort for cod of non-reporting countries (Method II in text).

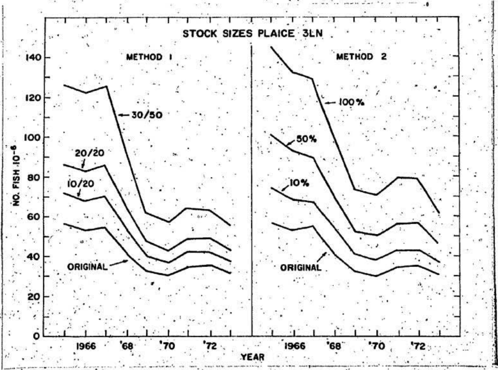

Fig. 37. Estimated stock size of plaice by the two methods described for Divisions 3LN.

quantities of flatfish were caught (Table 12). The net used by the pair trawler has a greater spread and was much higher (foot-rope to headline) than that used by Canadian otter trawlers. Nevertheless, in Division 3L 32% of the catch was American plaice and in Division 3O large quantities of yellowtail flounder were taken (Table 12). Division 3N data had too few hours to be meaningful, however, Canadian trawlers were more efficient at catching flatfish, these being the species sought (plaice and yellowtail). It should be pointed out, however, that catch and effort data for June-August 1973 for Spanish pair trawlers (ICNAF Stat. Bull. Vol. 23) gave catch per hour (tons) for cod at 0.962, 1.098 and 0.895 for Divisions 3L, 3N and 3O respectively. One can only speculate if more efficient catch rates for cod would also imply a higher rate for flatfish than in the recent commercial experiment. No information is available on possible plaice discards by the regular otter trawlers operated by Spain, Portugal and France (M).

New information recently became available from an operation by a local fishing company using new otter trawlers as pair trawlers and a net comparable to that used by Spanish pair trawlers. In the first experimental voyage the pair trawl caught 260,000 lb, 50% of which was plaice and most of the remainder cod. The boats were fishing in ICNAF Division 30 with many Spanish pair trawlers in the same locality apparently retaining only cod.

Discussion

Changes in abundance

For Division 3L the evidence points to a gradual decline in abundance. Stock size estimates and catch per unit effort both in weight and numbers (Fig. 31 and 32) point to a downward trend. For Division 3N, however, the pattern appears to be somewhat different with an apparent increase in abundance during the mid-1960's. The main fishing effort by the Newfoundland based fleet up to 1962 was for haddock with the primary effort in Division 3N. The decline in haddock abundance resulted in a diversion of effort to plaice. At this time, (1964) the more efficient stern trawler was introduced, and the directed effort was spread to the whole of the division (3N) so that the whole stock began to be exploited. During the mid-1960's in Division 3N then, the concentration of directed effort moved from southern localities to more northern locations on the eastern slope near 45°N latitude (Fig. 1).

While the increase in catch per hour in Division 3N may have been the result of an increase in fishing efficiency (q see page 90) and a change in location to previously lightly fished concentrations, the possibility of an increase in abundance should not be overlooked. If there was an increase in abundance because of strong year-class survival, this should be reflected in the catch per hour of fish that are fully recruited to the fishery and are making a major contribution to the total numbers caught. In neither Division was there any evidence of an increase in abundance of these age groups (Fig. 31B). In Division 3N the total catch per hour of fish 11 years and older does not indicate an increase in abundance that might be suggested from the catch per unit effort data and from stock estimations. Hence, as previously mentioned, the apparent increase in abundance during the mid 1960's can probably be explained by the fact that the early catches sampled only a part of the population and with a spread in effort to the entire stock there was an apparent increase in abundance. In other words only part of the stock was measured prior to 1963, and this was reflected in abundance estimates.

In Division 3L, however, excellent correlations were found between stock size and the catch per unit effort. The fishery here by the Canadian deep sea fleet has been almost exclusively for plaice with effort generally spread throughout the Division probably resulting in a good sampling of the population.

Stock assessment

Stock assessments made using 1972, 1973 data suggested that Grand Bank stocks were stabilizing at a level that would permit annual removals at about 48,000-52,000 tons for Divisions 3L and 3N combined. However, when the 1974 catch information was used in the analysis the rate of fishing (F) was found to be much higher than had been predicted and thus stock sizes in 1973 and 1974 on which 1975 projections were made were too high. The catch per hour in 1974 from reported catches also declined in 1974 (Table 9).

In addition to data from the analysis of commercial catches, research vessel data also provided supporting evidence of declining abundance of plaice on the Grand Bank, especially during 1973 and 1974. Thus research vessel surveys by the Newfoundland Biological Station (Pinhorn and Pitt 1974) and by Soviet research vessels (Chekhova 1974) also indicated lower abundance indices especially in Division 3L.

Bottom temperatures were very low in 1973-1974 and could have resulted in a higher rate of natural mortality or have caused them to move to localities where they were less available to the commercial fleet. However, it is difficult to see how this would not show up in the random fishing sets by research vessels.

A more plausible explanation could be an increase in the fishery for cod by the European fleet. As indicated previously, there is a probability of a high level of non-reported by-catch of plaice on the Grand Bank. If these removals remained proportional to the level of annual reported catches then one would not expect a rather sudden appearance of a high level of fishing mortality in a particular year. The occurrence of a high F would only occur if unreported removals were substantially higher say in 1973 in proportion to those in 1972 since the calculation of survival is basically a function of the ratio between catches of fish at age x in year n and n+1.

This is in fact what is suggested to have occurred during 1973. Adverse ice conditions during February and March 1973 resulted in a large amount of effort normally directed to cod in ICNAF Divisions 2J and 3K being diverted to the Grand Bank where local trawlers reported unusually heavy concentrations of Soviet effort on the northern half of the Grand Bank (Division 3L) during this period in prime plaice fishing localities. Official statistics did not, however, report unusually heavy catches of plaice. Added to this was the possibility of larger by-catches of plaice by Spanish trawlers fishing for cod, because plaice were abnormally concentrated because of unusual hydrographic conditions in localities where cod were also available.

Additionally, there is the suspicion that some of the large European countries lack the precise statistical systems necessary to report on catches from the various ICNAF divisions so that it is possible the data provided may be only guesses of just where the fish were caught.

The non-inclusion of substanial numbers of discards at all size ranges would cause an underestimation of stock size (Fig. 37). Thus the plaice stock has remained fairly high, at least up to 1972, in spite of the probably high removal level. Without a knowledge of total removals it is evident that a substantial proportion of the stock is not being managed, but is being removed at a level dependent on the effort expended by the countries that have relatively large cod quotas and the danger of this situation lies in the possibility that as cod become less abundant total effort might be increased to take the allocations with the resulting increase in the by-catch of plaice.

Another explanation that has to be considered is the possibility of a reduction in recruitment. Although stock abundance has been declining, this was observed primarily in fully recruited age groups and there was no evidence of large scale year-class failure.

SECTION 3 CHANGES IN GROWTH AND IN SIZE AND AGE AT SEXUAL MATURITY

Introduction

As previously indicated, the fishery for plaice on the Grand Bank began in the late 1940's and early 1950's. Since then the exploitation of this species has increased and as a result the stock size, particularly of the fully exploited age groups, has been considerably reduced.

This decrease in accumulated stock reduced competition and apparently brought about certain biological changes including an increase in growth and a reduction in the age at sexual maturity.

Methods

Abundance estimates

An account of methods used in estimating abundance is contained in the previous section and the data used here to make comparisons with changes in growth are identical to that previously presented.

Comparisons of growth curves

Because they have a longer life span than males and for simplicity in presentation, only female plaice were used in comparing growth curves for a series of years. Samples collected during the first half of the year only were used. Insufficient commercial data were available for 1969-72 to present curves for that period for Division 3N. Von Bertalanffy growth equations using a weighted least square fit (Allen 1966) were used. Research data were fitted from age 4 and over and commercial data from age 6.

The research data were secured by the Newfoundland Biological Station's vessel A.T. Cameron using a modified commercial 41-5 otter trawl with a lined cod end. Total catches were used when these were small or random or stratified sampling, selected from larger hauls. Except for 1971 and 1972 when the selection of fishing stations was by the stratified random method (Grosslein and Pinhorn 1971) fishing positions were at predetermined depths on transects across the slope of the bank.

Age and length at sexual maturity (M_{50})

The age at which plaice were sexually mature (M_{50}) was calculated using the procedure described by Bliss (1935 a and b and 1952) and described in Section 1. In this section and in Section 1, calculations of M_{50} were made for a number of localities for 1957-64 including the northeast and southeast slopes of the Grand Bank corresponding roughly to ICNAF Divisions 3L and 3N, respectively. Determination of sexual maturity was similar to that described in Pitt (1966).

Average length related to stock abundance and bottom temperatures

To relate differences in size at age to apparent change in abundance, the average length of females at selected ages and the asymptotic length grouping data in 4-year periods were plotted on stock size averaged for the same combination of years for research data L_{∞}, and average length at ages 5 and 10. For commercial data, asymptotic (L_{∞}) length and length at age 10 were used. The same length data were plotted on mean bottom temperatures averaged for the appropriate stations in the respective ICNAF divisions.

Results

Comparison of growth curves from research and commercial data

A gradual overall increase in the elevation of growth curves indicating an increase in mean size at age was evident (Fig. 38 and Table 13). Curves for research and commercial data from the same ICNAF division were slightly different since at younger ages, either through gear selectivity or discard, commercial vessels take a greater proportion of faster-growing fish at the younger ages. At the upper end of the age scale the commercial fleet sometimes discards large old fish because of possible jellied condition of the fish muscle.

In Division 3L, in commercial data for 1969-72, the size at age up to about age 12 was lower than in the two previous periods, possibly because recently processors have accepted smaller fish with resulting lowering of the discard rate.

Differences in size at age for selected year-classes and age groups of research data

A comparison in mean size at age for 1954-55 and 1960-61 year-classes (Fig. 39) utilizing ages on the relatively straight line portion (ages 6 to 11 or 12) of the von Bertalanffy growth curve indicated no significant difference between the slopes (rate of growth). In all cases, however, there was a significant difference between adjusted means (elevation). Similarity between rates of growth for different pairs of year-classes would appear to indicate that the initial growth period was probably critical in establishing size at a particular age, and beyond this period there was not a great deal of difference in annual growth increments. Unfortunately insufficient fish below age 4 were sampled to give a good idea of what happens during the early growth period.

Average size of plaice of various age groups has also increased over the 14-year span (1959-72) for which data were available (Fig. 40). In all cases, significant positive correlations were found in the plot of average size on a time scale. In some cases, howe-

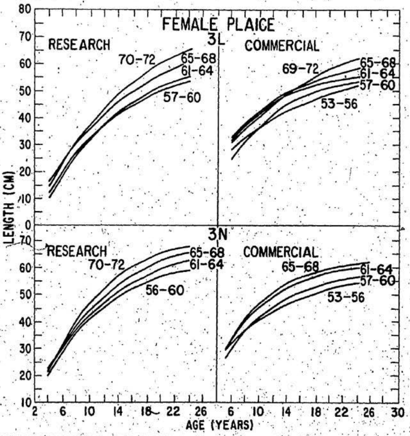

Fig. 38. Growth curves of female plaice for research and commercial data for ICNAF Divisions 3L and 3N.

Table 13. Parameters of growth curves in Fig.38. Values in brackets are standard errors.

Period	K	L_∞	t_0
Commercial Div. 3L			
1953-56	0.088 (0.018)	59.413 (2.424)	-0.690 (1.783)
1957-60	0.127 (0.014)	57.014 (1.233)	1.579 (0.689)
1961-64	0.125 (0.023)	58.613 (2.094)	-0.235 (1.239)
1965-68	0.097 (0.018)	63.510 (3.022)	-0.504 (1.232)
1969-72	0.069 (0.021)	80.000 (3.122)	-0.541 (1.212)
Commercial Div. 3N			
1953-56	0.090 (0.017)	59.533 (2.087)	-2.250 (1.341)
1957-60	0.124 (0.014)	60.711 (1.647)	0.166 (0.656)
1961-64	0.138 (0.011)	62.974 (1.427)	0.251 (0.370)
1965-68	0.135 (0.011)	65.182 (1.465)	0.384 (0.314)
Research Div. 3L			
1957-60	0.083 (0.004)	64.221 (1.361)	1.350 (0.113)
1961-64	0.084 (0.007)	65.900 (2.285)	1.781 (0.271)
1965-68	0.067 (0.009)	77.522 (5.369)	0.395 (0.317)
1969-72	0.076 (0.010)	80.200 (4.269)	1.351 (0.222)
Research Div. 3N			
1957-60	0.108 (0.004)	64.189 (0.984)	0.389 (0.120)
1961-64	0.093 (0.004)	70.385 (1.057)	-0.018 (0.116)
1965-68	0.099 (0.007)	72.938 (2.178)	0.404 (0.167)
1969-72	0.125 (0.009)	72.520 (1.832)	1.456 (0.111)

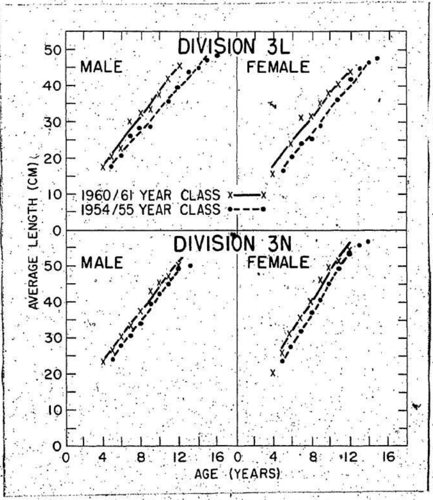

Fig. 39. Growth of 1954-55 and 1960-61 year-classes of plaice from research samples.

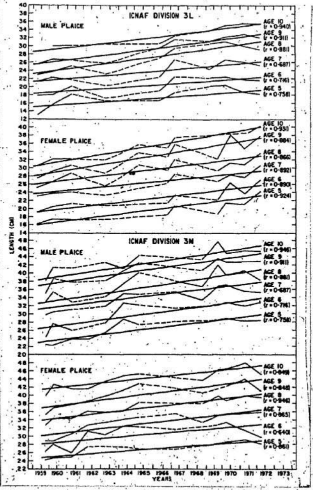

Fig. 40. Trends in growth of selected age groups of American plaice.

size on a time scale. In some cases, however, standard errors of the estimates of the line of best fit were fairly large. The upward trend nevertheless was quite apparent.

Changes in length related to stock size

In relating length at age to stock abundance significant correlations were found between L_∞ and stock size for both commercial and research data ($P = 0.04$ and 0.05 respectively) from Division 3L (Fig. 41 and 42). For the other relationships from 3L, significant correlations were found for the average size at age 5 and 10 for research data and for age 10 of the commercial data (omitting 1969-72 data) ($P < 0.05$ in all cases). For Division 3N no significant correlations were found, probably attributable to the somewhat variable nature of stock abundance estimates as previously explained (p 123-124).

Temperature trends and size at age

To document possible environmental changes that may have influenced the size of plaice in Divisions 3L and 3N, a series of water temperature observations from selected stations considered to be representative of the two divisions was used (Fig. 43).

Little change in mean bottom temperatures throughout the whole period is apparent (Station 27) (Fig. 43),

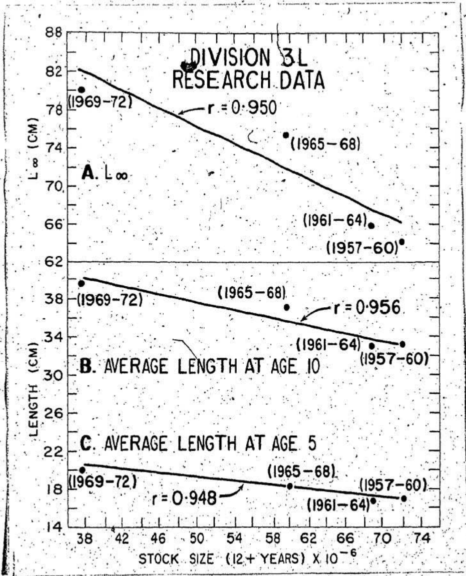

Fig. 41. Relationship between stock abundance, asymptotic length (L_∞) and average size at ages 5 and 10 years for research data from Division 3L.

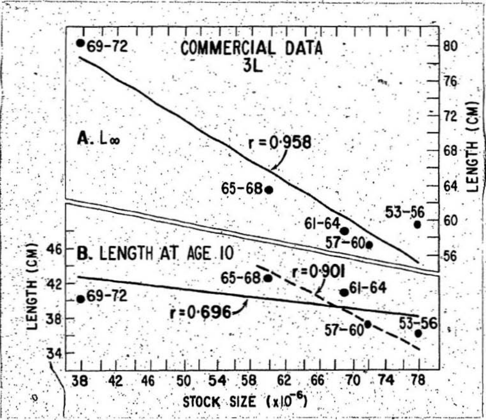

Fig. 42. Relationship between stock abundance, asymptotic length (L_∞) and average size at age 10 for commercial data from Division 3L.

although average temperatures for the last two periods were slightly higher than in the two previous ones. In the upper 25 metres, except for relatively high average temperatures for 1969-72, no trend was evident. For the three other Stations, 30, 36 and 37A (Fig. 43) in Division 3L no real trends were evident either in average bottom temperature or for the upper layer. In Division 3N, except for relatively high average temperatures at the upper layer in 1969-72 possibly because of Gulf water incursions, no real trends were evident at the more southerly stations (Fig. 43). Average values for Divisions 3L and 3N indicating the probable temperature conditions for the different periods are as follows:

Years	Division 3L		Division 3N	
	(A)	(B)	(A)	(B)
1950-52	-0.74	7.65	0.69	11.00
1953-56	-0.30	7.26	1.42	10.51
1957-60	-0.24	7.91	0.72	10.75
1961-64	-0.16	7.00	0.75	8.85
1965-68	-0.41	8.29	1.64	10.56
1969-72	-0.16	8.30	1.15	11.42

(A) Bottom temp. (B) Surface - 25 m.
3L average of stations 27, 36 and 37A; 3N average of Stations 30, 32 and 33 (Fig.43).

No significant correlations were found between average temperature and the various age-length parameters tested in the relationship with stock abundance ((Fig. 41 and 42). However, some positive trends were evident in

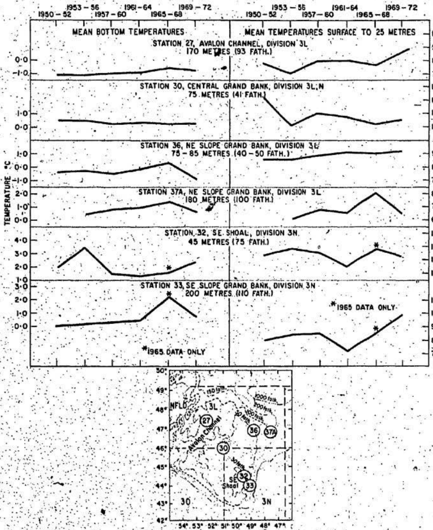

Fig. 43. Water temperatures from selected hydrographic stations for ICNAF Divisions 3L and 3N.

Division 3L data and those giving the highest correlation coefficients are shown in Fig. 44. For commercial data asymptotic length (L_∞) on mean bottom temperature of the previous period (i.e. L_∞ for 1953-56 on temperature for 1950-52) gave an r value of 0.848 ($P > 0.07$) and a similar plot for research data gave r values of 0.768 ($P < 0.20$) for L_∞ and 0.878 ($P < 0.10$) for the age 10 fish. For other plots of Division 3L data r values were below 0.750. Correlations with average temperatures surface to 25 metres gave approximately the same trends but with slightly lower coefficients. For Division 3N no significant correlations were found and in fact negative trends were found with upper layer temperatures.

Age and length at sexual maturity

The age of 50% maturity in 1969-72 was significantly lower than in the earlier period in both ICNAF Divisions (Table 4). In Division 3L the M_{50} for males changed from 7.59 ± 0.23 in 1961-65 to 6.43 ± 0.13 in the recent data, and a corresponding change from 13.98 ± 0.23 to 10.57 ± 0.18 for females. In Division 3N the decline was from 5.32 ± 0.13 to 4.65 ± 0.07 for males and 11.07 ± 0.15 to 8.79 ± 0.07 for females. P was < 0.001 in all cases.

There was no significant difference between the lengths at which male plaice were 50% mature for the two

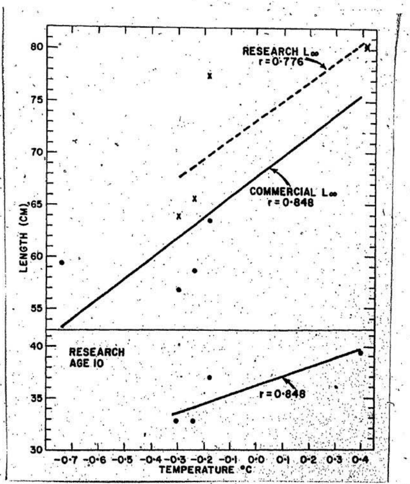

Fig. 44. Relationship between mean bottom temperature and L_∞ and average length at age 10 for Division 3L.

Table 14. List of ages and lengths at 50% maturity for American plaice for ICNAF Divisions 3L and 3N showing comparison for two time periods.

ICNAF Division	Year	Male					Female				
		Age		Length			Age		Length		
		M_{50}	$S\bar{x}$	From curve M_{50}	Calc M_{50}	$S\bar{x}$	M_{50}	$S\bar{x}$	From curve M_{50}	Calc M_{50}	$S\bar{x}$
3L	1961-65	7.59	0.23	25.52	23.46	0.65	13.98	0.23	41.50	42.14	0.39
	1969-72	6.43	0.13	26.00	23.91	0.29	10.57	0.18	41.10	40.36	0.19
3N	1957-64	5.32	0.13	25.49	23.97	0.48	11.07	0.15	43.71	43.31	0.38
	1971	4.65	0.07	25.30	25.58	0.66	8.79	0.07	42.80	41.45	0.86

periods in each area (P = 0.30 for Division 3L and 0.06 for Division 3N) (Table 14). Actually, for both periods and areas there was little difference in length at sexual maturity. For the females there was also no significant difference between the length at M_{50} for the two periods and areas (P = 0.30 for Division 3L and 0.10 for 3N).

Discussion

Changes in growth

Within the whole Northwest Atlantic there is a fairly high degree of variability in the length at age of plaice. In Section 1 and in Pitt (1967) it was shown that female plaice collected in research cruises varied significantly in size at age for a number of localities sampled. A positve correlation was found between size at ages 5 and 15 for the various localities and the probable bottom temperature (Section 1, Fig. 15).

The evidence presented here indicates a gradual increase in size at age during the period under consideration. Growth curves (Fig. 38) show a consistent increase in elevation although the standard errors (Table 13) of the various parameters suggest that some of the curves would overlap if the upper and lower values were put into the equation. Trends, however, are quite evident and coupled with the evidence from age groups and year-classes (Fig. 39 and 40) confirm the fact that an increase in size at comparable age has occurred.

Growth of fish depends ultimately upon the availability and utilization of food. Environmental conditions such as temperature control the utilization of food, but as McKenzie (1934 and 1935) and Kohler (1964) indicated for cod, temperature was related to growth indirectly inasmuch as it controlled the food supply. The previously mentioned association between average size at age and temperature for a number of geographic regions (Pitt 1967) suggests that temperature conditions control ultimate fish size probably to a great extent by its influence on the availability of prey species both in quantity and type assuming a relatively stable stock size.

Available hydrographic data (Fig. 43) suggest a fairly stable temperature regime within the two Divisions during the period considered here. No significant correlations were found between temperature and various age-length parameters. However, certain positive trends suggesting an increase in size at age with temperature were observed in Division 3L. The difficulty with temperature information used with so few data points is that anomalous conditions in one or two adjacent years can mask a general trend. The latter is particularly applicable to Division 3N where incursions of Gulf Stream water produce abnormal conditions in certain years. It is therefore suggested that changes in size at age may be to a large extent the result of a reduction in the density of plaice or other competing species. The evidence for Division 3L was particularly strong with significant correlations between size and stock abundance (Fig. 42 and 43), however, some caution should be exercised in putting too much credence in the relationship with asymptotic length (L_{∞}) since it may be susceptible to change depending upon the range of ages used in fitting the curve.

While there is no evidence that stock density per se influenced rate of growth of plaice on the Grand Bank, there is information in the literature indicating that crowding may affect the feeding of fish; thus Brown (1957) showed that *Salmo trutta* fry did not feed well in the presence of larger fish and that overcrowded fish ate less and utilized food less efficiently than fish in less crowded conditions. However, Kohler (1964) found that food supply was the main factor influencing growth. Sonina (1965) stated that while factors such as temperature and other conditions of the sea may exert an influence on growth, the primary cause of an increase in growth of Barents Sea haddock (Gadus aeglefinus) was a reduction in abundance and May (MS 1966) indicated a similar condition for cod (Gadus morhua) off Labrador (Divisions 2J-3K).

Not only were plaice reduced in numbers, but also competitors such as cod and haddock have been heavily exploited thus changing various interspecific relationships. Capelin and launce are major food items for plaice (see Section 1 and Pitt 1973) and a reduction in cod density would be expected to increase the abundance of these two prey species.

For American plaice below 30 cm, I found that the greatest percentage of total food (weight) was crustaceans principally amphipods and cumaceans followed closely by small brittle stars (Ophiuroidea) and other echinoderms (Section 1). Above 30 cm fish, principally launce and capelin accounted for the greatest proportion of the total diet, by weight although in Division 3L echinoderms are still a major item and the larger fish still competes with the smaller fish. The difference in average size at age beyond the first four or five years is not all that large and no significant difference was found between the rate of growth (slopes) for the 1954-55 (ages 5 to 15) and 1960-61 (ages 4 to 9) year-classes (Fig. 39). Elevation (size at age) apparently was determined at a fairly early age when plaice were feeding mainly on crustaceans and other small bottom forms. Obviously with a limit on the particle size that can be taken the density of the prey animals is important with competition from both large and small plaice and from other bottom feeders. Yanulov (1962) attributed the slow growth of plaice on the northern half of the Grand Bank (Division 3L) to high abundance and an inadequate food supply.

Size and age at sexual maturity

The apparent increase in size at age over a six or seven year period resulted in a significant reduction in the time required to attain sexual maturity. This suggests that gonad development is a function of body size with hormones that initiate sexual maturity being produced only when the fish and hence the gonads have reached a certain size or level of development. However, in spite of this, I found (Section 1 and Pitt 1966) that plaice from the southwest slope of the Grand Bank (mostly Division 3O), although they were larger at comparable age, matured at a greater age than those from slower-growing localities. Plaice from Flemish Cap (Division 3M) which had by far the largest size at age matured at significantly lower ages than those from any other locality (Section 1 and Pitt 1966). Fleming

(1960) showed that although cod off Labrador had the slowest rate of growth for the entire Newfoundland-Labrador area, they matured at a lower age.

The relationship between fish size and the attainment of sexual maturity is not entirely clear. However, Alm (1959), in a summary of literature and of his own experimental work, states that any particular species, stock or population that in the beginning exhibits a good rate of growth generally reaches sexual maturity at an earlier age than a stock with a slower initial rate. He also pointed out, however, that age of sexual maturity could be genetically determined thus explaining the early maturation of small fish in certain species. Karlander (1932) observed that when a heavy fishery drastically reduced the population size of the flounder (Pleuronectes flesus) in the Baltic, an acceleration in growth and a reduced age at sexual maturity by one year occurred. Gross (1949) with the same species reported that the fertilization of a sea loch improved feeding conditions, increased growth and also lowered age at sexual maturity. As previously noted, the major change in size at age in Grand Bank plaice appeared to be in the initial years and this could trigger an early maturation.

GENERAL CONCLUSIONS

The research program on the biology of Hippoglossoides platessoides has produced at least some of the information required for the management of the Grand Bank stock. Thus, there is evidence that while American plaice have a wide distribution throughout the Northwest Atlantic, Grand Bank plaice apparently are a discrete stock or a stock complex. Additionally there is evidence to support the management of Grand Bank plaice as a number of groups within the whole Grand Bank complex. Mature fish groups intermingle little, but are probably somewhat interdependent in the pre-metamorphosis stages. However, present methods of statistical reporting and enforcing of catch quotas necessitatel management at the ICNAF Division (or group of divisions) level.

Studies of spawning, and age and length at sexual maturity indicated differences which have to be considered in estimates of total spawning biomass. Similarly, fecundity studies may be important in future attempts as establishing possible stock-recruitment relationships.

As further background information for the management of this species a study of food requirements shed some light on the reason for differences in growth between different regions of the Grand Bank and pointed to the need for more detailed study of its ecology.

Research on this exploited stock on the Grand Bank hence was concerned directly or indirectly with the ultimate goal of eventually controlling fishing activity in a manner that would produce the highest average annual catch on a continuing basis. This level is usually termed the level of maximum sustainable yield. However, this is difficult to define with precision and really cannot be estimated on a long-term basis with any degree of accuracy with the information and models presently available.

In the early days of ICNAF, attempts were made to regulate fishing by limiting the size (age) of the fish recruited to the fishery, however more recent strategies of management have involved limiting removals from the stock by international catch quota regulations and thus hopefully regulating fishing mortality (F). A more recent event has been to impose direct effort limitations in combination with catch quotas.

Historically, in fish population dynamics studies, two measures of fishing mortality (F) have been defined, i.e. F_{max} and F_{msy}. F_{max} refers to a level of F at which the average catch (weight) from each recruit to the fishery is a maximum for a particular set of growth, age at first capture, and natural mortality parameters; and as such, for these conditions independent of recruitment. F_{msy} on the other hand refers to fishing mortality at which the average long-term catch from the stock as a whole is highest and hence involves recruitment levels. If at F_{max} the stock size is such as to produce the maximum level of recruitment then $F_{max} = F_{msy}$. The equating of these has usually been the practice in the ICNAF area in the absence of direct evidence of a stock-recruitment relationship.

The F_{max} point on the yield-per-recruit curves for American plaice is rather indefinite since the curves are essentially flat-topped (Fig. 29, page 99), and occurs only at high values of F. Because of this, a level of F lower than F_{max} (F_{msy}) was chosen as a reference point, i.e. $F_{0.1}$. This level is by definition close to the economic level (Gulland and Boerema 1972 and Anon. 1972). Fishing at this level should result in a larger average stock size and very little reduction in average catch as compared to fishing at F_{max}. There has been a general acceptance of $F_{0.1}$ by the international scientific community involved with giving advice to ICNAF for at least those stocks having flat-topped yield-per-recruit curves.

The determination of annual total allowable catches for American plaice on the Grand Bank was by calculating the annual level of removals corresponding to a fishing mortality of $F_{0.1}$ having first made certain assumptions concerning recruitment to the fishery. For the latter the only recourse was to use the average catch in numbers of the youngest age group appearing in the fishery for the previous 2 to 4 years.

Lack of precise information concerning recruitment is a major drawback. However, prospects for realistic estimates may be forthcoming from indices of abundance from stratified research vessel surveys (Page 5) by the Newfoundland Biological Station begin to produce results that can correlate pre-recuited age groups from research cruises with subsequent catches by the commercial fleet.

The apparent density-dependent changes in length and thus weight at age observed is illustrative of one of the basic concepts in fisheries population dynamics which is that a reduction in population size (numbers) from a virgin state is usually beneficial since the average weight of the remaining fish increases and this is the basic aim of fisheries management; to produce the greatest amount of weight from each recruit to the fishery on a long-term basis.

At present the effects of changing environment is largely ignored in the models and also the fact that fisheries rarely involve a single species.

The latter is especially so for demersal fisheries and in particular the fishery for American plaice on the Grand Bank where the fishery is carried out in conjunction with fisheries for yellowtail flounder (<u>Limanda ferruginea</u>) and cod (<u>Gadus morhua</u>). Thus future models for fisheries management will have to include additional parameters than those presently employed.

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Appendix 1 - Pope's Cohort Analysis

As with Gulland's and Jones' methods, Pope's (1972) Cohort Analysis is based on the two relationships

$$N_{i+1} = N_1 \exp\,[-F+M] \quad \text{............} \quad (1)$$

$$\text{and} \quad C_i = \frac{N_i F_i\,[(1-\exp\{-(F_i+M)\}]}{F_i + M} \quad \text{............} \quad (2)$$

where C_i = catch in year i, N_i population in year i, F and M = fishing and natural mortality, and exp = the exponential function, (1) above can be written as

$$N_{i+1}\exp(+M) = N_i \exp(-F_i) \quad \text{............} \quad (3)$$

$$= N_i - N_i\,(1-\exp\{-F_i\}) \quad \text{..........} \quad (4)$$

Rearranging (2) to solve for N_i and substituting into (4) for N_i

$$= N_i - C_i \left[\frac{(F_i+M)\,(1-\exp\{-F_i\})}{F_i[1-\exp\{-(F_i+M)\}]} \right] \quad \text{..........} \quad (5)$$

Within the range $M < 0.3$ and $F \leq 1.2$ the function in the large bracket can be approximated by exp(+M/2) which according to Pope has an error always less than 4%. The Cohort Analysis method is thus based on No. 5 above which is written as:

$$N_i = N_{i+1}\exp(+M) + C_i \exp(+M/2) \quad \text{..........} \quad (6)$$

which is rewritten as:

$$N_i = N_{i+1}e^M + C(e^{M/2}) \quad \text{............} \quad (6b)$$

Thus using 6 as a recurrence relationship

$$N_i = C_i e^{M/2} + C_{i+1} e^{3M/2} \dots\dots\dots + N_i e^{(t-i)M}$$

If the year-class has not passed completely through the fishery, C_i refers to the catch in year t only. In this case

$$N_t = \frac{C_t Z_t}{F_t (1-e^{-Z_t})} \qquad \text{(Baranov's catch equation)}$$

When the year-class has passed completely through the fishery C_i refers to the catch in year t and all subsequent years. In this case

$$N_t = \frac{C_t Z_t}{F_t}$$

F_i is calculated from

$$\text{Log}_e \left(\frac{N_{i+1}}{N_i} \right) -M$$

Cohort Analysis

Table I (a) and (b) and Table II (a) (b) (c) illustrates work sheets for this method and a step by step procedure for the calculations is provided. The data used are the catches of the 1957 year-class including ages 8-14 (Table II (a)) and the 1962 year-class using ages 6-12 (Table II (b)), M = 0.25. Matrices of catch population number and F from a typical printout are presented in Table II.

Step 1 For the oldest age group assume or estimate some value for F or F_n in Table I (a) for the 1957 year-class $F_n = 0.40$. Catches are listed in Col. (1) (C_i).

Step 2 (Col.2) For M = 0.25 calculate values of $C_i e^{M/2}$ for each age ($e^{M/2} = 1.1332$) and for age 14 Table III 161 x 1.1332 = 182.

Step 3 Calculate initial value of $N(N_i)$. In this case of $C_i (C_{14})$ (Table I (a)) the catch represents the virtual population since apparently the year-class has passed completely through the fishery. In this case the initial value of N_i is calculated from

$$N_i = \frac{C_i Z_i}{F_n}$$

$$N_{..} = \frac{C_{14} Z_{14}}{F_{14}} = \frac{161 \times (0.40 + 0.25)}{0.40} = 262$$

However, if the year-class was not complete as in the case of the 1962 year-class (Table I (b)), the expression

$$N_t = \frac{C_t Z_t}{F_t(1-e^{-Z}t)} = \frac{432(0.25 + 0.98)}{098(0.7077)}$$

$$N_{12} = 766$$

[The use of 0.98 as a starting F for this calculation is discussed later.]

Step 4 Calculate $N_{i+1}e^{M}$ (Col. 3)

For the 13 year olds in the 1957 year-class the calculation is simply 262 x e^{M} (1.284) = 336

Step 5 Calculate N_i(Col.4) = $N_{i+1}e^{M} + C_i e^{M/2}$

$$N_{13} = 336 + 131 = 467$$

Step 6 Calculate F by taking natural logs of Z and subtracting M

$$\frac{N_i+1}{N_i} = \frac{N_{14}}{N_{13}} = \frac{262}{467} = 0.558$$

$$Z_{13} = |\text{Log}_e\ 0.558| = 0.580$$

$$F_{13} = 0.580 - 0.25 = 0.330$$

Appendix 1 Table I. Calculation of Pope's cohort analyses $M = 0.25$

$F_n = 0.45$

(A) 1957 year-classes

Age	(1) C_i ('000)	(2) $C_i e^{M/2}$	(3) $N_{i+1} e^M$	(4) N ('000)	(5) $\mathrm{Log}_e \frac{N_{i+1}}{N_i}$	(6) F
8	1976	2238	15,841	18,080	0.382	0.132
9	3991	4522	7,816	12,338	0.707	0.456
10	1891	2143	3,944	6,087	0.684	0.434
11	1449	1641	1,430	3,072	1.014	0.764
12	454	514	600	1,114	0.869	0.619
13	116	131	336	467	0.558	0.330
14	161	182		262		0.400*

*Assumed value

(B) 1962 year-classes

Age	(1) C_i ('000)	(2) $C_i e^{M/2}$	(3) $N_{i+1} e^M$	(4) N ('000)	(5) $\mathrm{Log}_e \frac{N_{i+1}}{N_i}$	(6) F
6	159	180	25,157.3	25,337	0.2571	.007
7	2413	2734	16,858.9	19,593	0.4003	0.150
8	1449	1642	11,488.0	13,130	0.3836	0.134
9	2002	2269	6,678.1	8,947	0.5425	0.292
10	1650	1869	3,332.0	5,201	0.6953	0.445
11	1422	1611	983.5	2,595	1.220	0.970
12	432	489		766		0.981

Calculation of Matrices of Population Number (N) and Fishing Mortality (F)

From matricies of catch in numbers at each age for a number of years for both sexes in each of the two ICNAF Divisions values of (F) and population numbers (N) were calculated (Table II) using Pope's cohort analysis method starting at the oldest year-class as indicated in the example worked out in the latter appendix.

Estimation of Starting or (terminal) F_t.

As indicated, to initiate the calculation an assumed value of the exploitation rate is necessary. This is a difficult parameter to estimate especially for the more recent data. For the older data with year-classes that have passed completely through the fishery, some indication of starting or "terminal" F (F_t) can be obtained from the survival rate of the oldest ages providing reasonably accurate data on the effective fishing effort are available. In fact, the accuracy of F_t is not particularly sensitive for these data as evidenced from the following table which compares population and fishing mortality estimates for a portion of the 1951 year-class (Division 3L) using 5 different values of F_t.

TABLE ii

A POPULATION SIZE

AGE					
14	36,013	35,875	35,780	35,710	35,658
15	24,196	24,083	24,005	23,948	23,906
16	16,261	16,168	16,104	16,059	16,023
17	7,597	7,521	7,469	7,431	7,402
18	3,296	3,234	3,192	3,161	3,137
19	1,582	1,531	1,497	1,471	1,452
20	555	514	485	464	448
21	236	202	187	161	148

B FISHING MORTALITY

AGE					
14	.198	.199	.199	.200	.200
15	.197	.198	.199	.200	.200
16	.561	.564	.568	.571	.572
17	.634	.644	.650	.654	.658
18	.534	.547	.557	.564	.570
19	.847	.892	.927	.953	.975
20	.656	.735	.802	.858	.907
21 F_z =	.450	.550	.650	.750	.850

Except for those for age 21 the amount of difference in stock size is not very substantial when one considers the probable errors in the estimates of numbers caught.

However, for recent data the estimation of F_t is difficult and may only be accomplished by reference to the effort level of the recent year in the regression of F on fishing effort from historic data (section 11 Fig. 34). However, since some of the early effort data were not particularly good, the fit of the line may not be especially accurate.

Having determined a starting on terminal Fishing mortality rate (F_t), calculations can proceed as described in this Appendix doing each year-class separately. However, when calculations are initiated for year-classes that have not completely passed through the fishery some method had to be used to arrive at a value for F_t. In Table iii c as a starting value for the 1951 year-class the average F for 1967-73 (1.725) (horizontally across the table) was used as F_t and gave a population size of 93 (Table III b). As each year-class is completed diagonally in Table III c, the values for the seven years are averaged to give a new F_t.

However, averaging Fs in this way is probably correct only if the fishery is fairly stabilized without fluctuations in fishing effort and/or recruitment. This rarely the case and is very likely not the case for Grand Bank plaice.

The averaging of F and the calculation of matrices of F in this manner was used to get an indication of <u>partial recruitment</u> levels, or an array of the exploitation pattern expressed as a proportion and from these, values of F_t could be calculated that probably more closely reflected current fishing levels. From an examination of the mean F values in Table III (c), it would appear that plaice are being recruited to the fishery throughout their exploited phase so that in estimating proportions that were being fully exploited (partial recruitment) it was assumed that the F value at age 11, 0.684, was equal to 1.0 and levels of recruitment were calculated on this basis. Thus, taking an assumed F_t for the oldest age in the most recent years data, the partial recruitment values can be applied to give F_t to initiate the computations. Thus, in Table III (c) the starting values on the right side would be used instead of the 1967-73 average.

Appendix 1, Table III. Matrices of (a) Catch, (b) population and (c) fishing mortality.

(a)

x10⁻³ → $\times 10^{-3}$

Age \ Year	1967	1968	1969	1970	1971	1972	1973	1974
6	1,216	159	363	461	437	905	477	218
7	3,671	2,457	2,413	881	630	654	869	2,932
8	1,976	3,224	1,382	1,449	1,490	2,470	2,449	3,578
9	2,359	3,991	4,382	3,130	2,002	2,260	2,574	2,356
10	2,552	2,136	1,891	2,112	2,192	1,650	1,563	1,393
11	1,184	1,410	344	1,449	841	1,150	1,422	959
12	1,448	904	369	154	454	542	1,017	432
13	576	806	356	233	43	116	869	70
14	193	49	102	100	50	2	161	20

(b)

$\times 10^{-3}$

Age	1967	1968	1969	1970	1971	1972	1973	1974
6	32,044	25,337	21,450	21,494	22,285	43,954	52,390	11,503
7	31,438	23,882	19,593	16,385	16,333	16,970	33,433	40,380
8	18,084	31,244	16,031	13,130	11,983	12,164	12,639	25,270
9	6,937	12,340	13,700	11,577	8,947	8,017	7,294	7,682
10	6,413	3,321	6,089	6,802	6,254	5,201	4,249	3,409
11	3,666	2,742	701	3,073	3,434	2,936	2,595	1,930
12	3,087	1,810	891	242	1,114	1,932	1,272	766
13	755	1,126	612	368	53	467	1,026	93
14	314	80	166	163	81	3	262	33

(c)

Age / Year	1967	1968	1969	1970	1971	1972	1973	Average F 1967-73	Partial Recruitment	F_t
6	0.044	0.007	0.019	0.025	0.022	0.024	0.010	0.022	0.03	.012
7	0.142	0.124	0.150	0.063	0.045	0.045	0.030	0.085	0.12	.048
8	0.132	0.189	0.100	0.134	0.152	0.261	0.248	0.174	0.25	.100
9	0.487	0.456	0.450	0.366	0.292	0.384	0.511	0.420	0.62	.248
10	0.599	1.305	0.434	0.434	0.506	0.445	0.539	0.608	0.89	.356
11	0.456	0.873	0.812	0.764	0.325	0.586	0.970	0.684	1.0	.40
12	0.758	0.834	0.633	1.272	0.619	0.382	2.365	0.981	1.43	.572
13	1.99	1.666	1.076	1.262	2.539	0.330	3.203	1.725	1.30	.520
14	0.400	0.400	0.400	0.400	0.400	0.400	0.400	0.400		.40