

ERRATA

ICNAF Research Bulletin, No. 13

1. In the first column of page 83, the paragraph preceding "Results" should be replaced by the following:

Let \hat{X}' be an unbiased estimate of X' (where $X' = \ln X$) with a normal distribution with mean X' and variance σ^2 . The expected value of X is

$$E(X) = e^{X' + \sigma^2/2} \quad (6)$$

This method (Brownlee, 1965) was used to estimate α , β , $(\alpha\beta)$, $(\alpha\gamma)$ and $(\beta\gamma)$ from the regression coefficients estimated for Equation (3). The 95% confidence intervals of these coefficients were obtained by taking the antilogarithm of the end points of the 95% confidence intervals of α' , β' , γ' , $(\alpha\beta)'$, $(\alpha\gamma)'$ and $(\beta\gamma)'$.

2. On page 85, "Equation (7)" in the heading of Table 2 should be changed to "Equation (6)".

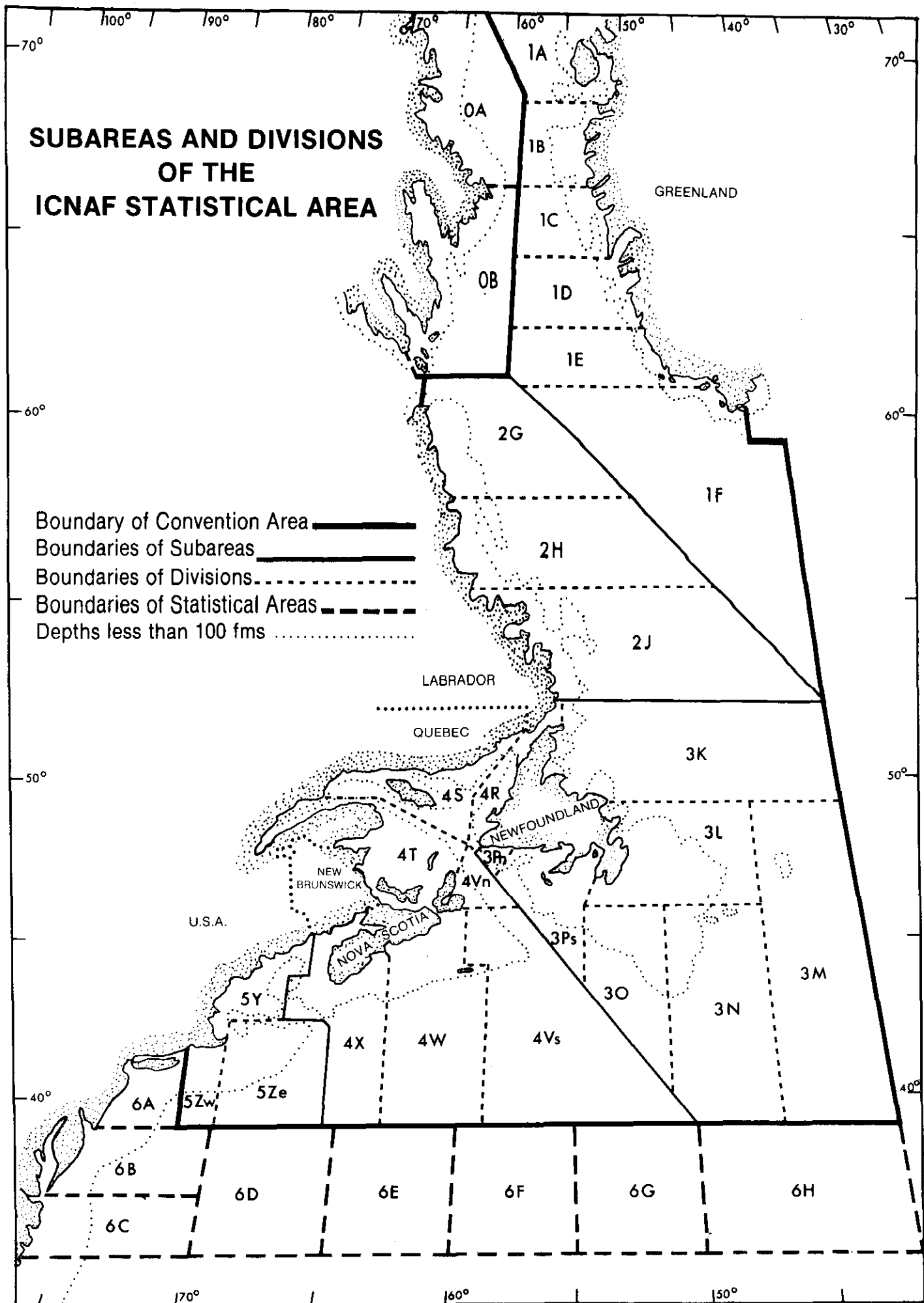
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SUBAREAS AND DIVISIONS OF THE ICNAF STATISTICAL AREA

- Boundary of Convention Area
- Boundaries of Subareas
- Boundaries of Divisions
- Boundaries of Statistical Areas
- Depths less than 100 fms

LABRADOR
 QUEBEC
 NEW BRUNSWICK
 NOVA SCOTIA
 NEWFOUNDLAND
 U.S.A.

1A 1B 1C 1D 1E 1F
 2G 2H 2J
 3K 3L 3M 3N 3O 3P 3Ps 3R 3S 3T 3V 3Vn 3Vs 3W 3X 3Y 3Z
 4A 4B 4C 4D 4E 4F 4G 4H 4I 4J 4K 4L 4M 4N 4O 4P 4Q 4R 4S 4T 4U 4V 4Vn 4Vs 4W 4X 4Y 4Z
 5A 5B 5C 5D 5E 5F 5G 5H 5I 5J 5K 5L 5M 5N 5O 5P 5Q 5R 5S 5T 5U 5V 5W 5X 5Y 5Z
 6A 6B 6C 6D 6E 6F 6G 6H

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Age and Growth of the Greenland Halibut, *Reinhardtius hippoglossoides* (Walbaum), in ICNAF Subareas 2-4

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Abstract

Length and age distributions and growth curves are presented for Greenland halibut of ICNAF Subareas 2-4. The largest and oldest Greenland halibut were caught in the most northerly areas. There was little difference in growth rate between males and females for sections of the growth curves presented here. The growth rate generally increased from north to south.

Introduction

The Greenland halibut, *Reinhardtius hippoglossoides*, is distributed from the Arctic area southward to the Scotian Shelf in the northwestern region of the Atlantic and prefers temperatures of about -1°C or higher, usually -0.5° to 3°C in deep water over large areas (Templeman, 1973). Lear and Pitt (MS 1971) found them to be most plentiful at temperatures of -0.3° to 2.8°C in the deep bays of Newfoundland. Although they are known to migrate vertically, they are generally associated with the bottom and prefer depths of 235-565 m (Lear and Pitt, MS 1971).

In the Newfoundland and Labrador area, the only significant Greenland halibut fishery occurs in ICNAF Subarea 2 and Div. 3K and 3L. During the 1950's and 1960's the fishery for Greenland halibut occurred primarily in Subarea 3 and catches were taken exclusively by Canadian (Nfld.) inshore fishermen in White Bay, Notre Dame Bay and Trinity Bay, and to a lesser extent in Fortune Bay, using mostly longlines. More recently, because of reduced catches in the inshore areas, Canadian fishermen fish farther offshore in larger boats using monofilament gillnets (165-203 mm mesh). At present, only 15-20% of the annual Greenland halibut catch is taken by Canadian inshore fishermen, the remaining 80-85% being taken by the larger European fleet (Bowering and Pitt, MS 1975).

This paper presents the length and age distributions as well as the growth curves of Greenland halibut in ICNAF Subareas 2-4.

Materials and Methods

Most of the data were collected during all seasons of 1970-75 in regular survey cruises of the *A.T. Cameron*, a 51-m side trawler operated by the Newfoundland Biological Station. Some of the data in ICNAF Div. 3K was collected in October 1975 by the *M/V Shamook*, a 23-m stern trawler also of the Newfoundland Biological Station. The *Anton Dohrn* of the Federal Republic of Germany collected much of the data for ICNAF Div. 2J and 3K during a regular groundfish survey in November-December 1975. All ships used bottom otter trawl with a nylon liner (12.7-28.1 mm mesh) in the codend. All tows were of 30 minutes duration and only catch records for which no damage to the gear occurred were used in the analyses. Place names and areas referred to in the text are shown in Fig. 1.

Length (2-cm groups) and age frequencies are presented for males and females separately for each division or subarea concerned as percentages of the total catches in the various areas. Age determinations were made according to Lear and Pitt (1975). Since there appeared to be no year-class dominance or any major fluctuations in length and age composition from year to year, data for the years 1970-75 were combined for the analyses carried out.

Growth is expressed in terms of weighted linear least squares regressions of age on length, since the data did not appear to fit the von Bertalanffy growth equation. Growth curves are presented separately by sex for

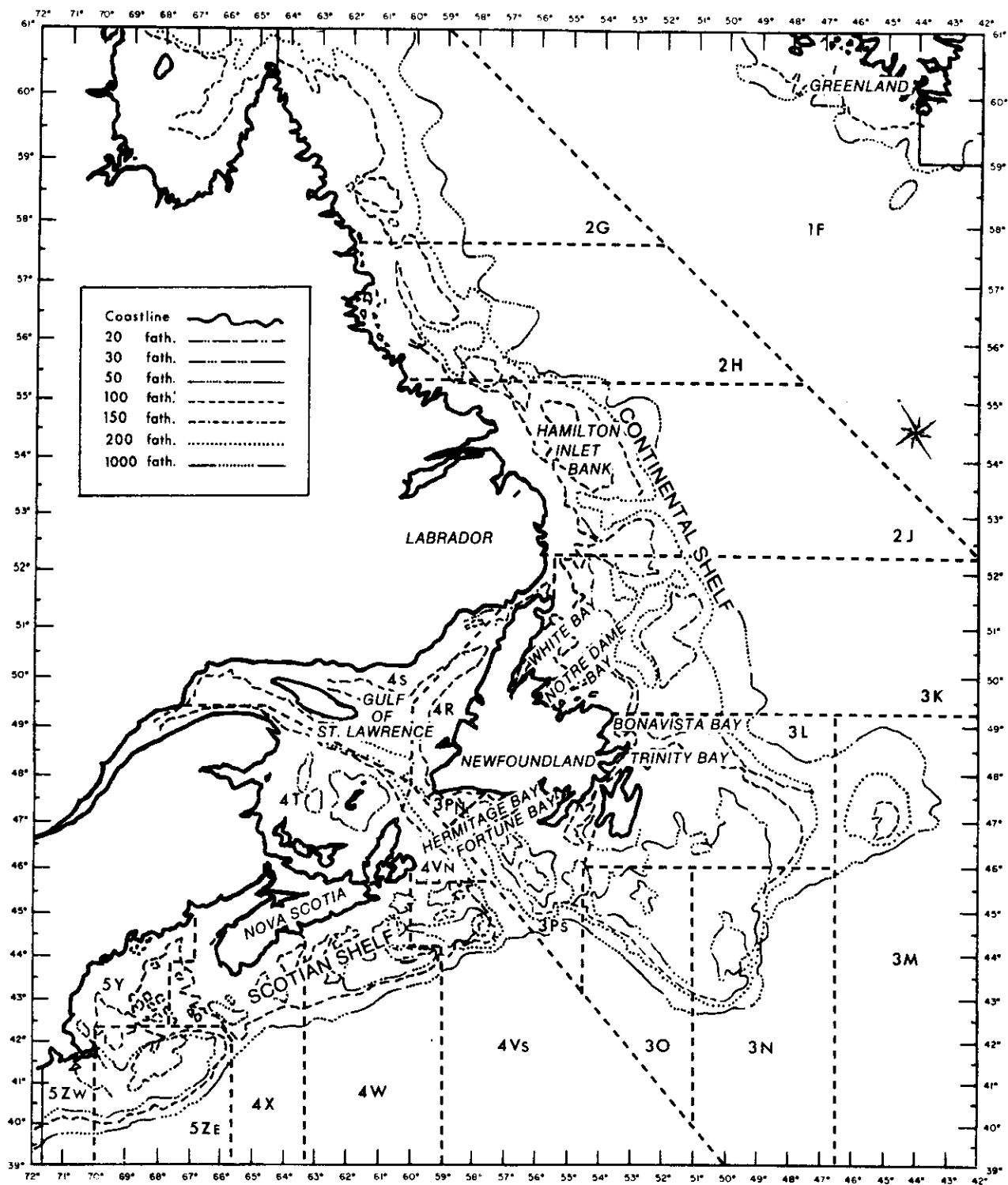


Fig. 1. Place names, fishing areas and ICNAF areas referred to in the text.

samples from each division or subarea to show similarities or differences in growth rate by sex and area.

Results

Length distribution

The males generally ranged from 8 to 70 cm and females from 8 to 80 cm for the southern areas to about 106

cm for the eastern and northern areas (Fig. 2). The smaller size group of 14-20 cm was predominant in all areas except Subarea 4 where the size groups were relatively proportionate throughout the range. There were more larger fish caught in the northerly areas than to the south.

Age distribution

In Subarea 2 there seemed to be little dominance of any particular age group (Fig. 3), however there were more

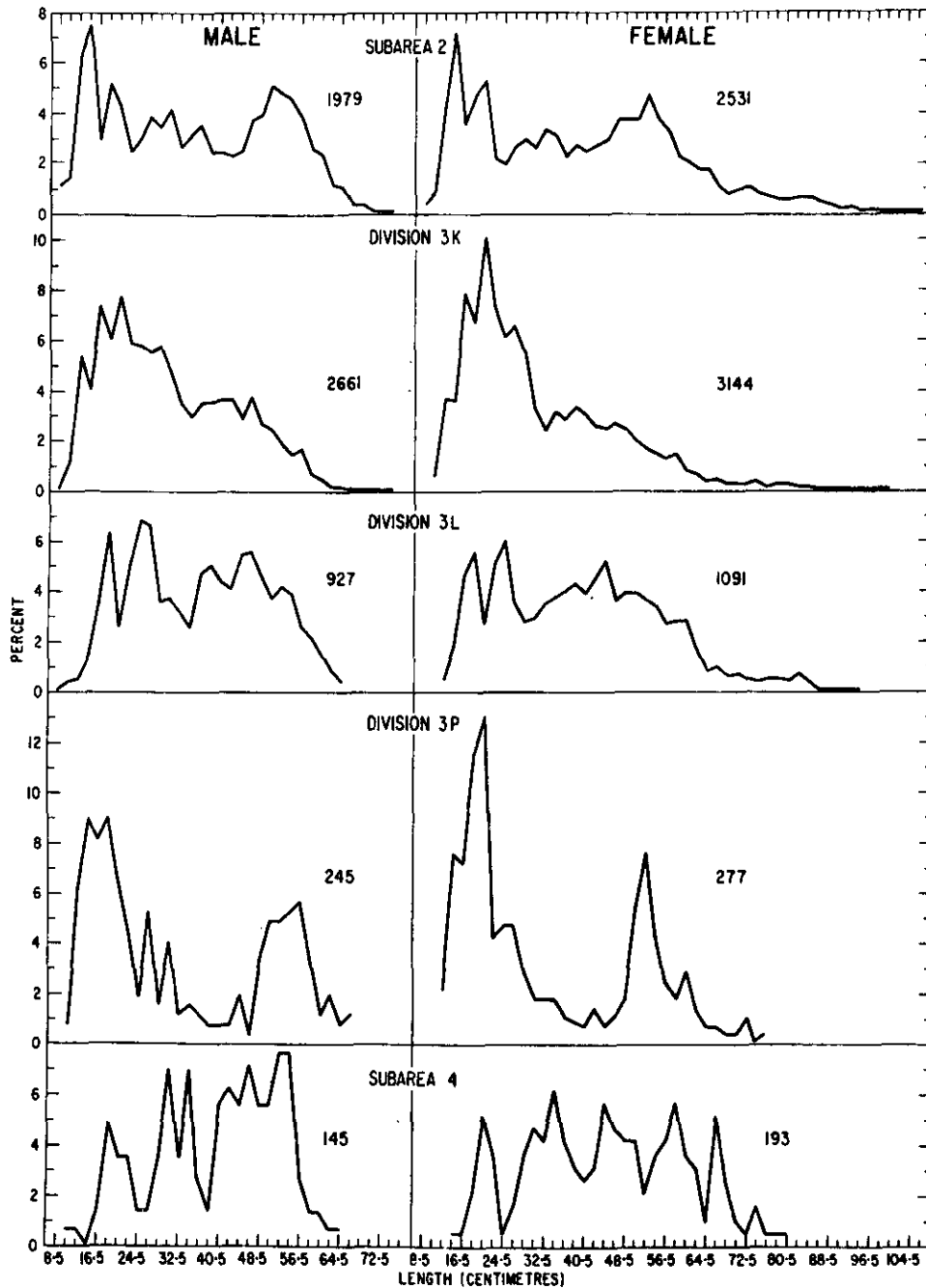


Fig. 2. Length distribution of male and female Greenland halibut taken by research vessel in Subareas 2 to 4, 1970-75.

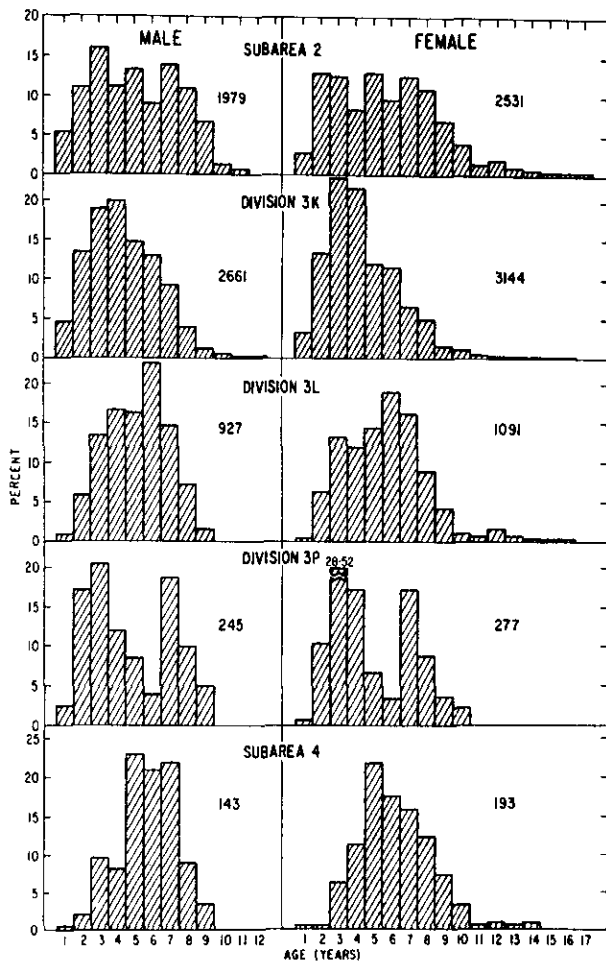


Fig. 3. Age distribution of male and female Greenland halibut taken by research vessel in Subareas 2 to 4, 1970-75.

older fish caught in Subarea 2 than any other area. All age groups from 2 to 9 were well represented for both sexes. In Div. 3K fish of age 3 and 4 appeared in higher proportions than any other age groups for both sexes, however, other age groups were reasonably strong in number. Catches in Div. 3L were dominated by fish of age 6 and those in Subarea 4 by fish of ages 5-7. In Div. 3P high proportions of ages 2-4 were prevalent with other age groups being low in number. No males older than age 12 were caught in any area and none older than age 9 in Subarea 4 and Div. 3L and 3P. The oldest females ranged from age 10 in Div. 3P to age 18 in Subarea 2.

Growth rates

Only in Div. 3K was there a statistical difference between the males and females at the 5% significance level (Fig. 4; Table 1) for ages where males and females were both represented in the growth curve. The difference however was very small (Student's $t = 2.2428$) and would probably be of very little practical importance. The fastest

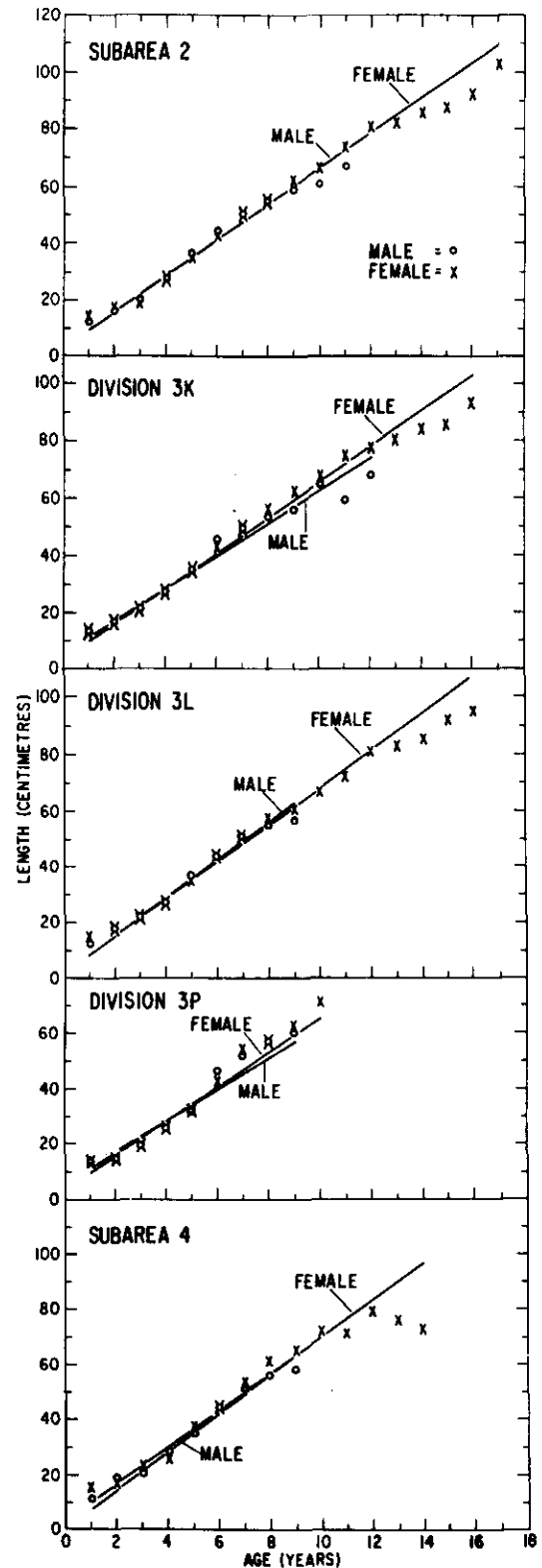


Fig. 4. Linear regressions of length on age for male and female Greenland halibut from five ICNAF areas.

growth rates for both males and females occurred in Div. 3P followed by those of Subarea 4 (Fig. 5). The growth rate generally increased from north to south, however, the males of Subarea 2 appeared to grow faster than those of Div. 3K.

Discussion

Having reached maturity, the Greenland halibut migrates to the deep edge of the continental slope zone whereas immature fish are found on the shelf and in the

deep bays (Zilanov *et al.*, MS 1976). Templeman (1973) indicated that spawning takes place in winter in the deep, warm waters between Canada and Greenland, with the larvae drifting to the south by the Labrador Current. Smidt (1969) has also suggested that the Greenland halibut found on the west coast of Greenland also move onto the deep warm water south of the ridge between Canada and Greenland to spawn. Zilanov *et al.* (MS 1976) has suggested that the whole Greenland halibut stock complex from Northwest Greenland south to the Grand Bank is in fact a single interbreeding stock. Since the largest and

TABLE 1. Parameters for regressions of length on age of Greenland halibut for ages where males and females occur together.

Area	Sex	No. of fish	Slope	Y-intercept	Corr. coeff. (r)
Subarea 2	Male	1,989	6.4234	2.5302	0.9925
	Female	2,411	6.5794	1.7781	0.9955
Div. 3K	Male	2,760	5.7682	5.0626	0.9742
	Female	3,105	6.4677	2.2875	0.9955
Div. 3L	Male	924	6.7873	1.4667	0.9917
	Female	1,039	6.8915	0.5272	0.9939
Div. 3P	Male	240	7.1713	-1.2686	0.9887
	Female	266	7.5199	-3.1907	0.9900
Subarea 4	Male	143	6.9365	0.4775	0.9900
	Female	181	7.7586	-2.9677	0.9924

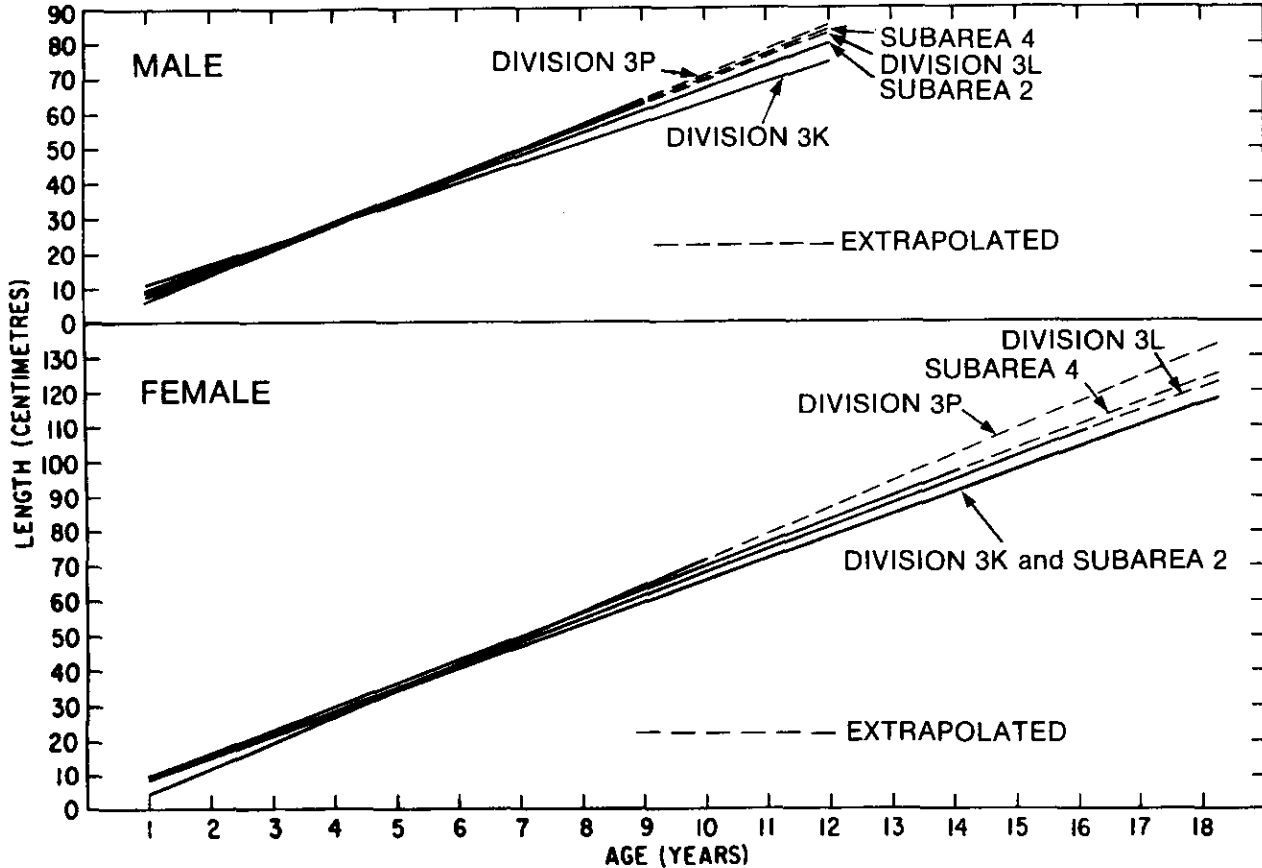


Fig. 5. Comparisons of linear regressions of length on age for male and female Greenland halibut from five ICNAF areas.

oldest fish are caught further north, it could possibly indicate a migration northward as the fish approach the spawning cycle.

Lear (MS 1970) has indicated that some spawning is evident in the Gulf of St. Lawrence (Subarea 4) but data are too scanty to suggest any connection with the northern areas. He found many small Greenland halibut in Hermitage Bay (Div. 3P) which could possibly be a nursery area for Greenland spawning in deep water to the south since no mature fish were found.

Unpublished data at the Newfoundland Biological Station have indicated that of all samples collected, both research and commercial, very few mature Greenland halibut have been caught. Since there was a complete absence of females over age 9 in Div. 3P and age 10 in Subarea 4, it may indicate that fish of those areas may mature much faster than those of the northern areas and migrate out into deeper waters beyond fishing limits. Pitt (MS 1974) indicated that tagged Greenland halibut migrate over very long distances and Greenland halibut tagged in Trinity Bay were found close to the edge of the continental shelf as far north as Hamilton Bank. It was not known, however, if these fish were maturing when recaptured and therefore could not substantiate the theory that they move north to spawn.

Differences in growth rate between males and females are generally the result of genetics which determine the physiology and behaviour of the fish rather than the result of the environment (Alm, 1959), since presumably the males and females are subjected to the same set of environmental conditions. Energy is diverted to the formation of sex products with little left for growth. Since few mature fish were caught (unpublished data of the Newfoundland Biological Station), the growth rates were relatively consistent for males and females throughout the sections of the growth curves presented in this study, thus explaining the linear relationship of age on length. The slight difference in growth rate of males and females of Div. 3K may be due to errors in age reading as otoliths taken from fish of this area are most difficult to interpret. Since, presumably, there are older, mature fish not being caught, this study deals only with that section of the growth curve below the inflection point and consequently estimates L_{∞} for the von Bertalanffy growth equation were not realistic and therefore could not be used.

There are many factors which influence the growth of fishes, the most important being food supply for only when sufficient food is available can a fish attain its maximum

size for existing environmental conditions. Factors such as temperature, density-dependence and abundance of competing species are generally a result of their effect upon food supply. Since there is a general increase in growth rate from north to south (Fig. 5) temperature would seem to be a contributing factor. Templeman (1964) indicated that the volume of warmer water increased from north to south because of the direction of the Labrador Current and therefore it is possible that temperature is an influencing factor. However, Greenland halibut not only migrate over long distances (Pitt, MS 1974) but are also known to make vertical migrations in search of food (de Groot, 1968; Lear, MS 1970) and are consequently subjected to a wide range of temperatures. When relating growth to environmental conditions, other conditions such as reductions in stock size, removals of competing species such as cod, and removals of food species such as shrimp and capelin must be considered. It is obvious therefore that interactions are very complex and to relate them to changes in growth with any degree of accuracy is extremely difficult.

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Predation of Cod, *Gadus morhua*, on Capelin, *Mallotus villosus*, off Eastern Newfoundland and in the Gulf of St. Lawrence

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Abstract

An analysis of the stomach contents of cod, *Gadus morhua*, collected in winter and summer of 1975 and 1976 off southwestern Newfoundland and in northeastern Gulf of St. Lawrence (ICNAF Divisions 3Pn, 4R and 4S) and off southern Labrador and eastern Newfoundland (Div. 2J, 3K and 3L) revealed that fish, especially capelin, *Mallotus villosus*, and crustaceans were the most important components of the diet of cod. Capelin is an important prey of cod during summer and winter in Div. 3Pn, 4R and 4S, whereas in Div. 2J, 3K and 3L capelin are consumed moderately in winter but not in summer on the offshore banks except in Div. 3L. No variation in the diet of cod was noted in relation to the sex of the predator. In Div. 2J, 3K and 3L, capelin were consumed by cod of nearly all size groups in relatively the same proportion, whereas in Div. 3Pn, 4R and 4S the amount of capelin consumed decreased with increasing size of cod, being replaced mainly by herring, redfish and American plaice. Calculations, based on estimated mean weights of ingested capelin, annual predation rate of capelin by cod and elimination rates of food by cod, indicate that cod consume from 0.8 to 1.3 times their weight of capelin annually in both regions. On the basis of average biomass estimates for cod during 1965-69 (prior to the large reduction in stock abundance in the early 1970's), the quantities of capelin ingested annually are estimated to be in the range of 2.0-3.4 million tons in Div. 2J, 3K and 3L and 240-400 thousand tons in Div. 3Pn, 4R and 4S.

Introduction

The feeding of cod in the Northwest Atlantic has been described in several studies. Those of Powles (1958) and Kohler and Fitzgerald (1969) provide valuable information for the southern part of the Gulf of St. Lawrence, and research by Templeman (1964), Stanek (MS 1975), and Seliverstov and Kovalev (MS 1976) contribute to the knowledge of feeding relationships between cod and capelin in the Labrador and eastern Newfoundland areas. However, little information on these relationships is available for the winter months.

This paper attempts to define the main characteristics of cod predation on capelin at two different times of the year and to estimate the quantities of capelin ingested annually, from data presented on the diet of cod taken on the banks off Southwest Newfoundland and in the northeastern part of the Gulf of St. Lawrence (Div. 3Pn, 4R and 4S) and on the banks off southern Labrador and eastern Newfoundland (Div. 2J, 3K and 3L).

Materials and Methods

The materials for this study were collected during three research vessels surveys: on board the *Cryos* off the southwest and west coasts of Newfoundland (Div. 3Pn and 4R) from 17 January to 24 February 1975, on board the

Thalassa in the northeastern Gulf of St. Lawrence (Div. 4R and 4S) and off Labrador and eastern Newfoundland (Div. 2J, 3K and 3L) from 8 July to 7 August 1975, and on board the *Cryos* off the west coast of Newfoundland (Div. 4R) and off Labrador and eastern Newfoundland (Div. 2J, 3K and 3L) from 8 January to 27 February 1976. A total of 106 trawling stations were occupied (Fig. 1) at depths ranging from 95 to 315 m in Div. 3Pn, 4R and 4S and from 130 to 445 m in Div. 2J, 3K and 3L.

On board after each haul, the cod stomachs were immediately removed from a sample of fish, quick frozen at -40°C in individual plastic bags and stored at -26°C to avoid deterioration of the contents. Fish showing signs of regurgitation or feeding when in the trawl were discarded. For each stomach collected, information on sex, total length (cm) and maturity stage of cod was recorded, together with details on the sampling station. In the laboratory, each stomach was weighed and the state of repletion estimated using the scale, 0, 1, 2, 3 and 4 for empty, quarter-full, half-full, three-quarters full and completely full respectively. After dissection, the food items were separated by species, or by systematic group (genus or family) if too far digested for identification at the species level. Each species or group was weighed to the hundredth of a gram and stages of digestion were noted using four categories ranging from food most recently ingested to food having been digested to a greater degree. A total of 1,307 cod stomachs (532 from Div. 2J, 3K and 3L

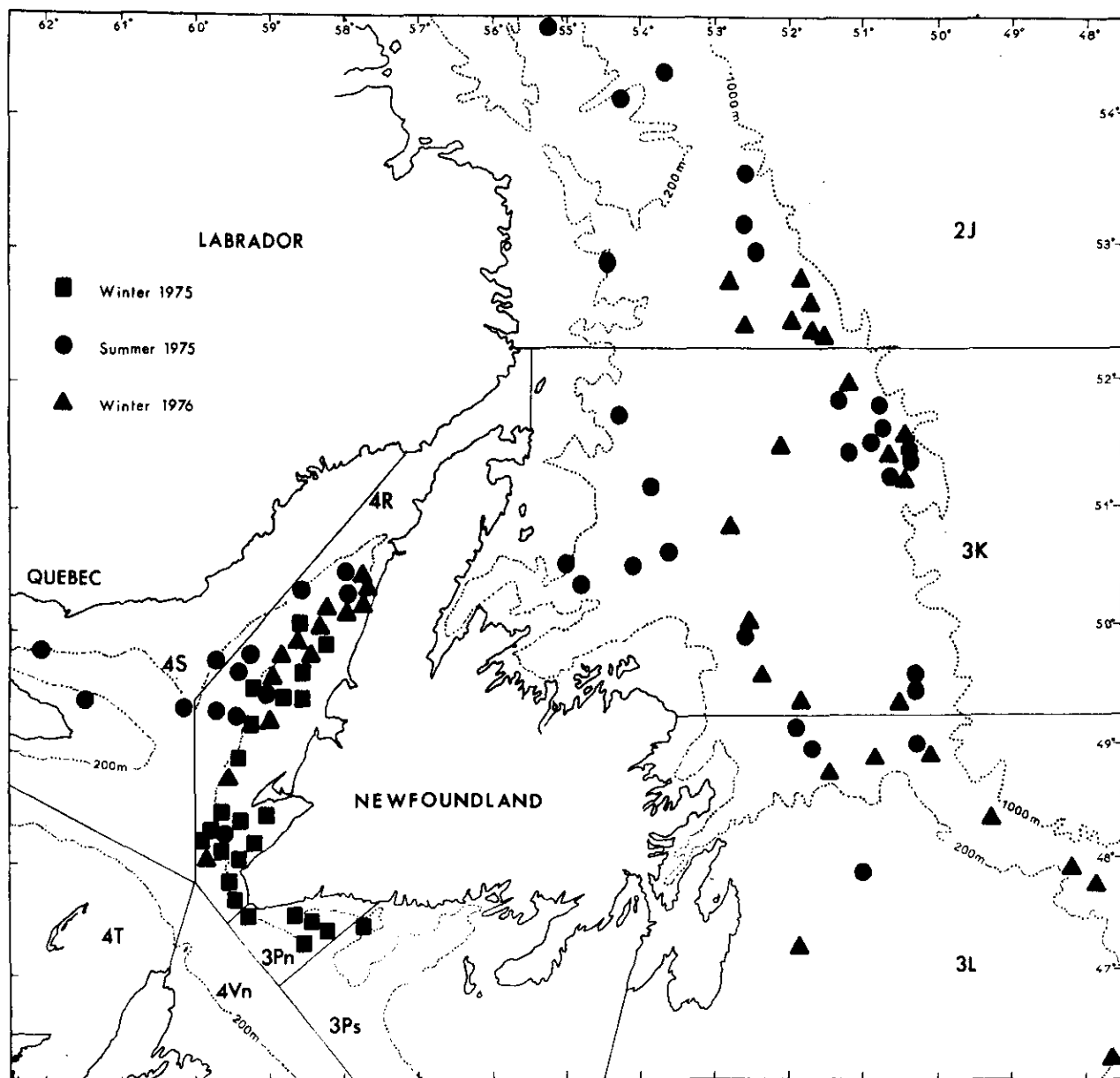


Fig. 1. Map showing the positions of trawling stations where cod stomachs were collected in 1975 and 1976.

and 775 from Div. 3Pn, 4R and 4S) were examined for this study, and the majority of them were found at repletion stages 3 and 4.

Diet of Cod

Food components of diet

Data obtained from the analysis of 1,292 non-empty cod stomachs from the six ICNAF divisions are given in Table 1, in terms of the percentage occurrence of the food items ingested. Among the five systematic groups found in the stomachs, fish and crustaceans were consistently the

most frequent, with annelids, molluscs and echinoderms present in most areas and seasons but much less frequently.

Teleosts were found in 82% of the cod stomachs, the most frequently occurring species being capelin (75%), followed by redfish (15%), lantern fishes (8%), American plaice (2.3%), Greenland halibut (1.6%), small cod (1.5%) and herring (1.2%). Other fish (9%) represented by 14 species were rare, each occurring less than 10 times.

Crustaceans, the second food group in occurrence (45%), were mainly represented by *Parathemisto*

TABLE 1. The diet of cod during summer and winter of 1975-76 in various ICNAF divisions, expressed as the percentage occurrence of food items in stomach samples.

Stomach contents	2J		3K		3L		3Pn		4R		4S
	Summer 1975	Winter 1976	Summer 1975	Winter 1976	Summer 1975	Winter 1976	Winter 1975	Winter 1975	Summer 1975	Winter 1976	Summer 1975
Annelida	15.5	5.9	5.2	10.2	4.3	2.9	1.0	6.1	—	0.4	—
Mollusca	12.1	11.8	4.4	23.5	4.3	5.9	1.0	9.2	1.4	1.6	2.1
— Pelecypoda	1.7	—	0.7	—	—	—	—	1.8	—	—	—
— Gasteropoda, Buccinidae	8.6	6.9	3.7	10.2	1.4	5.9	—	7.9	0.7	1.2	—
— Cephalopoda	1.7	4.9	—	14.3	2.9	—	1.0	—	0.7	0.4	2.1
Crustacea	91.4	74.5	61.5	93.9	38.6	36.8	32.7	39.9	19.7	23.3	25.6
— Amphipoda — Gammaridea	20.7	6.9	11.9	14.3	2.9	2.9	—	10.1	2.0	0.8	2.1
— Hyperiidea ¹	19.0	51.0	31.1	83.7	20.0	17.6	—	—	—	3.3	—
— Caprellidea	—	1.0	—	4.1	—	—	—	—	—	—	—
— Euphausiacea	3.4	1.0	2.2	—	4.3	—	27.6	13.2	5.4	4.5	4.2
— Decapoda — Pandalidae	53.4	33.3	30.4	30.6	18.6	14.7	2.0	18.4	11.6	12.7	19.1
— Paguridae	—	—	0.7	—	—	—	—	0.4	0.7	0.4	—
— Mairidae ²	31.0	—	5.1	4.1	1.4	5.8	2.0	3.5	0.7	0.8	2.1
— Others	17.2	1.0	2.1	18.3	1.4	—	2.0	3.0	1.4	4.8	—
— Mysidacea, Cumacea, Isopoda	3.4	2.0	1.4	9.2	1.4	1.5	3.1	—	—	—	—
Echinodermata	1.7	7.9	2.2	8.1	—	3.0	—	13.2	0.7	0.8	—
— Ophiuroidea ³	—	6.9	1.5	6.1	—	1.5	—	13.2	0.7	0.8	—
— Holothuroidea ⁴	1.7	1.0	0.7	2.0	—	1.5	—	—	—	—	—
Teleostei	32.8	65.7	63.7	51.0	98.6	85.3	98.0	82.9	98.6	97.6	95.7
— Clupea harengus	—	—	—	—	1.4	—	—	4.4	3.4	0.8	—
— Mallotus villosus	1.7	45.1	5.2	8.2	95.7	79.4	85.7	60.1	93.9	89.0	80.9
— Myctophidae	1.7	—	44.4	19.4	2.9	—	—	—	—	—	—
— Gadidae	10.3	1.0	1.5	2.0	2.9	2.9	—	1.8	—	2.0	2.1
— Sebastes mentella	—	3.9	1.5	6.1	—	—	31.6	26.8	11.6	12.2	8.5
— Cottidae	8.6	1.0	0.7	1.0	—	—	—	—	—	—	—
— Pleuronectidae	6.9	7.8	3.7	3.1	2.9	4.4	—	6.6	—	2.0	—
— Others	6.9	2.0	10.4	4.1	2.9	—	1.0	3.9	1.4	0.4	6.4
— Not identified	3.4	10.8	1.5	15.3	—	1.5	—	0.9	—	—	2.1
Others	—	5.9	—	1.0	—	—	—	3.1	—	—	—
Not identified	—	6.9	0.7	6.1	—	—	2.0	4.0	0.7	0.4	—
Pebbles and shell fragments	—	1.0	1.5	4.1	—	1.5	5.1	7.0	0.7	1.2	—
Number of cod stomachs with food	58	102	134	97	69	68	98	227	147	245	47

¹ Parathemisto guadichaudii; ² Hyas sp., Chionocetes opilio; ³ Ophiopholis aculeata; Ophiura sp.; ⁴ Thyone sp., Nesithuria intestinalis.

gaudichaudii (38%) and *Pandalus borealis* (38%), followed by the euphausiids *Meganyctiphanes norvegica* and *Thysanoessa* sp. (15%), the gammarid *Anonyx nugax* (14%), other shrimps *Pandalus montagui*, *Sabinea sarsi* and *Spirontocaris* sp. (9%), and crabs *Hyas* sp. and *Chionocetes opilio* (9%). Rarer groups (5%) were mysids, cumaceans, isopods, caprellids and hermit crabs (each occurring less than 10 times).

Molluscs were present in only 6% of the stomachs, represented mainly by the gasteropods *Buccinum* sp., *Neptunea* sp. and *Colus* sp. (68%), the cephalopods *Rossia* sp., *Gonatus fabricii*, *Illex illecebrosus* and *Bathypolypus arcticus* (32%), and some pelecypods *Chlamys* sp., *Yoldia myalis* and *Cyrtodaria siliqua* (8%). Echinoderms, sometimes present (4%), were mainly represented by the brittle star *Ophiopholis aculeata* (77%), and rarely by other items (32%) such as holothurians, sea urchins and other brittle stars. Annelids were also found on occasion (4%), including nereids, eunicids, and other unidentified groups. Rare food items grouped under

"Others" in Table 1 included sipunculids, cnidarians, ascidians and priapulids.

Geographical and seasonal variation in diet of cod

The weights of the various food items in the diet of cod expressed as percentages of the total weight of food in the stomachs from each area by season are given in Table 2, and the relative proportions of the major prey groups are illustrated in Fig. 2.

In Div. 3Pn, 4R and 4S, there was little variation in the diet of cod both seasonally and by divisions in so far as the major food items were concerned. The quantity of fish ingested was almost the same in winter (91%) as in summer (93%). Capelin was the most important food item in summer (78%) and also in winter (59%). Small redfish were ingested in all divisions, constituting 5% of the diet in summer and 19% in winter. Herring and American plaice were secondary prey species in Div. 4R only, the former being 13% of the diet in summer and 6% in winter, and the latter being about 4% in summer only. Besides fish, the next

TABLE 2. The diet of cod during summer and winter of 1975-76 in various ICNAF divisions, expressed as percentages of the weight of food items in stomach samples.

Stomach contents	2J		3K		3L		3Pn	4R		4S	
	Summer 1975	Winter 1976	Summer 1975	Winter 1976	Summer 1975	Winter 1976	Winter 1975	Winter 1975	Summer 1975	Winter 1976	Summer 1975
Annelida	1.2	0.2	0.4	0.1	0.1	—	—	0.5	—	—	—
Mollusca	1.9	1.2	0.7	9.0	3.7	0.1	0.2	1.1	0.3	0.1	0.4
— Pelecypoda	—	—	—	—	—	—	—	0.4	—	—	—
— Gasteropoda, Buccinidae	1.7	0.9	0.4	1.3	—	0.1	—	0.7	—	—	—
— Cephalopoda	0.2	0.3	0.3	7.7	3.7	—	0.2	—	0.3	0.1	0.4
Crustacea	73.4	22.8	24.3	31.8	2.5	5.6	5.0	7.2	5.6	5.2	7.5
— Amphipoda — Gammaridea	1.0	0.1	3.6	0.1	—	—	—	0.2	0.2	—	0.1
— Hyperidea ¹	5.5	12.6	7.4	24.0	1.3	1.1	—	—	—	0.1	—
— Caprellidea	—	—	—	0.1	—	—	—	—	—	—	—
— Euphausiacea	0.1	—	0.3	—	—	—	4.1	0.9	1.2	0.9	—
— Decapoda — Pandalidae	23.9	10.0	11.0	5.9	0.7	1.3	0.5	3.4	4.0	3.7	7.0
— Pagurodidae	—	—	0.1	—	—	—	—	0.2	—	—	—
— Mairidae ²	40.9	—	1.7	0.9	0.4	3.2	0.1	2.3	0.1	0.2	0.4
— Others	1.7	0.1	0.2	0.7	0.1	—	0.1	0.2	0.1	0.3	—
— Mysidacea, Cumacea, Isopoda	0.3	—	—	0.1	—	—	0.2	—	—	—	—
Echinodermata	0.1	1.3	0.9	1.3	—	—	—	5.8	—	0.6	—
— Ophiuroidea ³	—	1.3	0.8	0.9	—	—	—	5.8	—	0.6	—
— Holothuroidea ⁴	0.1	—	0.1	0.4	—	—	—	—	—	—	—
Teleostei	23.2	71.7	73.7	53.4	93.6	94.2	94.7	84.0	94.0	94.1	92.0
— Clupea harengus	—	—	—	—	0.1	—	—	11.3	12.9	5.8	—
— Mallotus villosus	0.8	55.3	3.5	13.8	90.3	81.7	64.7	39.9	75.6	71.0	79.3
— Myctophidae	0.2	—	59.4	24.3	0.5	—	—	—	—	—	—
— Gadidae	—	9.7	—	—	0.4	7.8	—	1.8	—	6.0	3.6
— Sebastes mentella	—	2.1	0.1	1.0	—	—	28.7	19.2	5.4	8.6	5.2
— Cottidae	6.8	0.3	—	0.4	—	—	—	—	—	—	—
— Pleuronectidae	1.3	2.0	3.9	4.4	1.4	4.4	—	8.6	—	2.7	—
— Others	13.0	0.2	6.6	2.9	0.9	—	1.3	3.0	0.1	—	3.9
— Not identified	1.1	2.1	0.2	6.6	—	0.3	—	0.2	—	—	—
Others	—	1.1	—	0.4	—	—	—	0.5	—	—	—
Not identified	—	1.5	—	3.4	—	—	0.2	0.2	—	—	—
Pebbles and shell fragments	0.2	—	—	0.5	—	—	—	0.7	—	0.1	—
Percentage total	100.0	99.8	100.0	99.9	99.9	99.9	100.1	100.0	99.9	100.1	99.9
Number of cod stomachs with food	58	102	134	97	69	68	98	227	147	245	47

¹ Parathemisto guadichaudii; ² Hyas sp., Chinocetes opilio; ³ Ophiopholis aculeata, Ophiura sp.; ⁴ Thyone sp., Nesothuria intestinalis.

most important food group was crustaceans (7% in summer and 6% in winter), mainly the northern deepwater prawn, *Pandalus borealis*. Brittle stars formed about 3% of the diet in winter in Div. 4R.

In Div. 2J, 3K and 3L, the diet of cod is more varied than differences (Table 2, Fig. 2). On the northern part of the Grand Bank (Div. 3L), fish formed the greatest part of the diet (94% in both seasons) mainly due to heavy predation on capelin in summer (90%) and even in winter (82%). Other fish, mainly small cod (8%) and Greenland halibut (4%) were consumed in winter. Small quantities of squids (4%) were found in the stomachs in summer, while crustaceans were present in summer (3%) and winter (6%). Off Northeast Newfoundland (Div. 3K), fish formed the greater portion of the diet in summer (74%) and to a lesser extent in winter (53%), consisting mainly of lanternfishes (59 and 24% respectively). Unlike the other areas considered, capelin constituted only 4% of the diet in summer and 14% in winter. Crustaceans formed 24% of the

summer diet (11% amphipods and 11% northern deepwater prawn). Off southern Labrador (Div. 2J), the diet of cod in summer consisted largely of crustaceans (73%) with fish (23%) as the secondary food group, whereas in winter fish (72%) and crustaceans (23%) were the most important food items. Capelin constituted 55% of the diet in winter but only 0.8% in summer in this area. Other fish items included small cod (10% in winter) and cottids (7% in summer). Crustaceans in the summer diet consisted mainly of crabs (41%) and northern deepwater prawn (24%), whereas this group was represented in the winter diet by amphipods (13%) and northern deepwater prawn (10%). Annelids, molluscs and echinoderms were sometimes present but in very small quantities.

Variation in diet relative to sex and size of cod

The weights of the food items in the diet of cod from all areas, expressed as percentages of the total weight of food in the stomachs for each sex and season, are given in

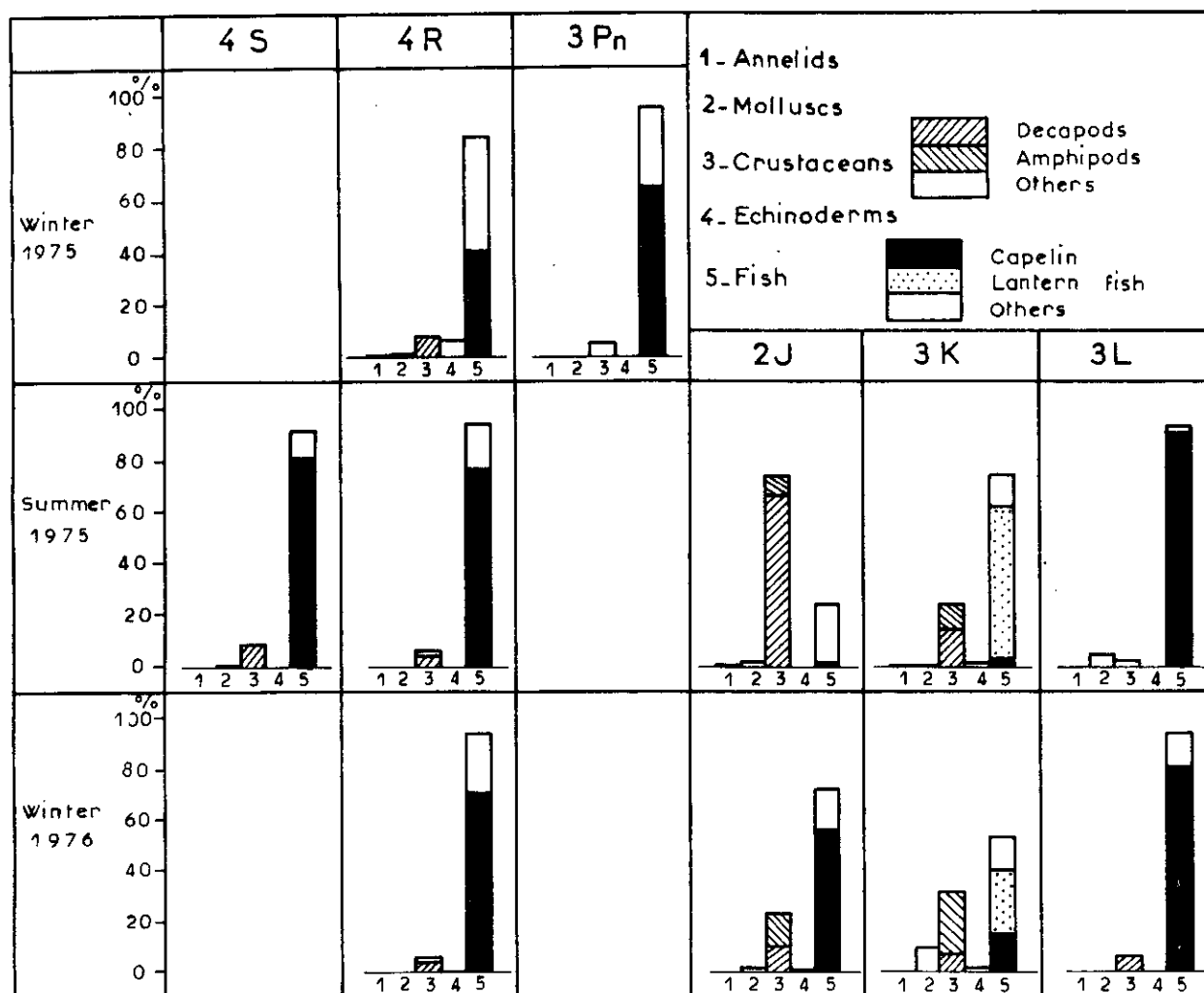


Fig. 2. Geographic and seasonal variations in the diet of cod by divisions, expressed as percentages of the weight of food items ingested.

Table 3. The results indicate that the diets of male and female cod are very similar in each of the seasons considered. Consequently, the data for males and females were combined to study the variation in diet in relation to size of predator in each of the major regions (Div. 2J, 3K and 3L and Div. 3Pn, 4R and 4S). The results are detailed in Table 4 and summarized by major food groups in Fig. 3.

The diet of young cod (16-25 cm), present only in the samples from Div. 2J, 3K and 3L, consisted mainly of small crustaceans (89%) represented by *Parathemisto gaudichaudii* (36%), small shrimps (29%) and gammarids (17%). Polychaetes (9%) and capelin (2%) formed the remainder of the diet. In cod larger than 25 cm, the diet was essentially composed of fish (72-99%) in both regions, except for four cod of 86-95 cm in which the stomach contents consisted almost entirely of crabs (66%) and cephalopods (30%). However, there was considerable variation in the type and quantity of some fish species ingested by cod larger than 25 cm in each region.

In Div. 2J, 3K and 3L, predation on capelin was relatively stable over all length groups, the percentages being 59, 54 and 56% of the diet in cod of length groups 26-55, 56-75 and 76-115 cm respectively (Fig. 3). Thus the actual quantities of capelin ingested increased with size of cod. Predation on lanternfishes increased in importance with size of predator up to 46-55 cm (17% of diet) but declined to 7% in 76-85 cm fish and none were found in larger sizes (Table 4). In contrast, cod larger than 65 cm fed more on young cod and Greenland halibut.

In Div. 3Pn, 4R and 4S, predation on capelin declined greatly from 89% in 26-55 cm fish to 55% in 56-75 cm fish and to 13% in larger cod (Fig. 3), whereas predation on other fish species increased. However, despite the decline in percentage of capelin ingested, the actual quantities consumed by cod of different size groups may have been relatively stable, as the ingested quantities increase with size of the predator. Predation on herring was not found in cod less than 55 cm but increased rapidly in importance

TABLE 3. Comparison of the diets of male and female cod in summer and winter of 1975-76 for all areas combined, expressed as percentages of the weight of food items in the stomach samples.

Stomach contents	Summer		Winter	
	Male	Female	Male	Female
Annelida	0.1	0.3	0.1	0.2
Mollusca	0.5	2.2	0.8	1.1
— Pelecypoda	—	—	—	0.1
— Gasteropoda, Buccinidae	0.1	0.3	0.4	0.3
— Cephalopoda	0.4	1.9	0.4	0.7
Crustacea	15.7	14.8	11.0	8.2
— Amphipoda — Gammaridea	0.5	1.1	0.1	—
— Hyperiidea ¹	3.3	1.6	3.3	3.2
— Caprellidea	—	—	—	—
— Euphausiacea	0.3	0.6	1.5	0.4
— Decapoda — Pandalidae	7.3	6.1	3.5	3.9
— Paguridae	—	—	—	0.1
— Maiidae ²	3.8	5.2	2.4	0.4
— Others	0.4	0.2	0.2	0.2
— Mysidacea, Cumacea, Isopoda	0.1	—	—	—
Echinodermata	0.2	0.1	1.9	1.5
— Ophiuroidea ³	0.2	0.1	1.8	1.5
— Holothuroidea ⁴	—	—	0.1	—
Teleostei	83.5	82.3	85.4	88.0
— Clupea harengus	5.0	3.9	5.3	3.6
— Mallotus villosus	58.1	60.3	61.9	59.5
— Myctophidae	8.9	12.7	1.4	1.7
— Gadidae	1.0	—	4.7	5.1
— Sebastes mentella	2.6	2.0	6.5	11.9
— Cottidae	0.2	1.0	—	0.1
— Pleuronectidae	2.7	0.3	2.8	4.9
— Others	4.7	2.0	1.7	0.6
— Not identified	0.3	0.1	1.1	0.6
Others	—	—	0.1	0.4
Not identified	—	—	0.6	0.3
Pebbles and shell fragments	—	—	0.3	0.1
Percentage total	100.0	99.7	100.2	99.8
Number of cod stomachs with food	213	242	384	453

¹ Parathemisto guadichaudii; ² Hyas sp., Chionocetes opilio; ³ Ophiopholis aculeata, Ophiura sp.; ⁴ Thyone sp., Nesothuria inestinalis.

from 0.4% in 56-75 cm fish to 57% in 96-105 cm and to 85% in 2 cod greater than 105 cm (Table 4). Small quantities (1-3%) of young redfish were eaten by 26-45 cm cod, but the proportion of this species in the diet increased to 26% for larger cod, especially those of 76-95 cm. American plaice were not found in the stomachs of cod less than 45 cm but represented 8% of the diet in 56-75 cm fish and 10% in larger fish. Young cod were not found as food in the stomachs of cod less than 56 cm but formed 6% of the diet, on the average, in larger fish.

Other fish species were variously found in the stomachs of cod from both major regions but the quantities were too small to use as the basis for conclusions on quantities consumed in relation to size of predator.

Cod Predation on Capelin

Mean weight of capelin ingested in a meal

The results of the previous section indicated that predation of cod on capelin varies with the size of the predator. Consequently, it was necessary to consider this variation in estimating the average consumption of capelin. The mean weight (P_m) of capelin ingested by cod of each length group (Table 5) was determined from the weight of capelin in stomachs which had been observed in repletion stages 3 and 4 (i.e. three-quarters full and completely full). The length frequencies used were those obtained from the measurement of 12,814 cod in Div. 2J, 3K and 3L and 5,484 cod in Div. 3Pn, 4R and 4S during the 1975-76 surveys. The estimates of the average weight of capelin ingested in one

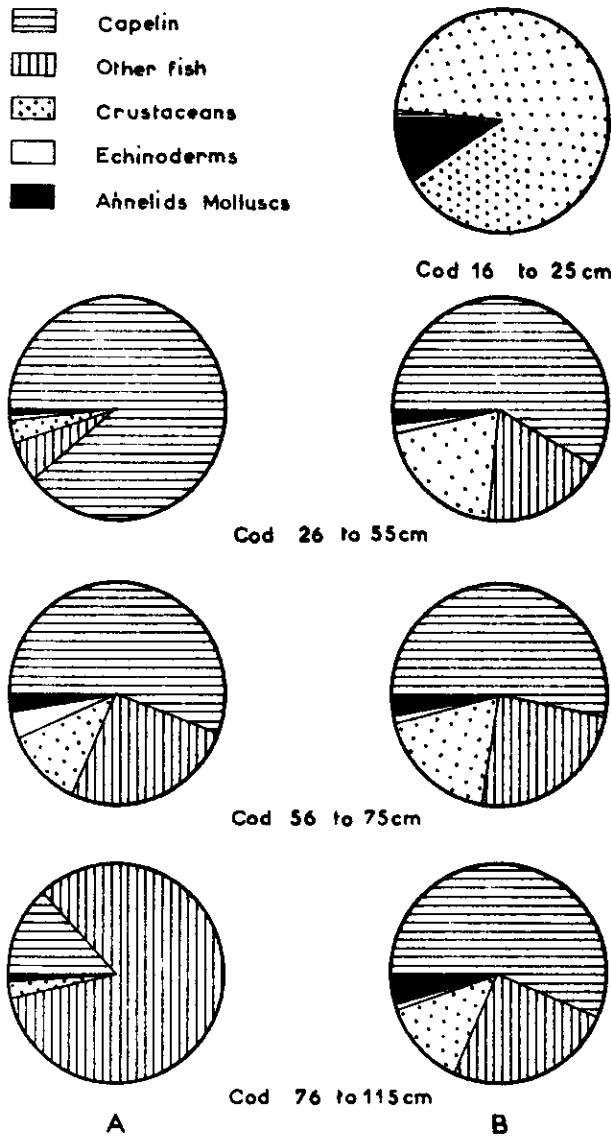


Fig. 3. Variation in the diet of cod in relation to size of predator in (A) Div. 3Pn, 4R and 4S, and (B) Div. 2J, 3K and 3L.

meal by an average cod are 27.8 and 29.4 g for Div. 2J, 3K and 3L and Div. 3Pn, 4R and 4S respectively (Table 5).

Mean weight of capelin ingested annually

The mean weights of capelin consumed in one meal by an average cod were calculated from samples collected in two periods of the year when the geographical distribution of the two species is such that the availability of capelin as a prey for cod is greater than in other periods. Indeed, after both species have migrated southwest along the west coast of Newfoundland, they are found in winter intermingling off Southwest Newfoundland (Div. 3Pn and 4R). Similarly for the populations in Div. 2J, 3K and 3L, after the offshore migration of both species in the autumn, they

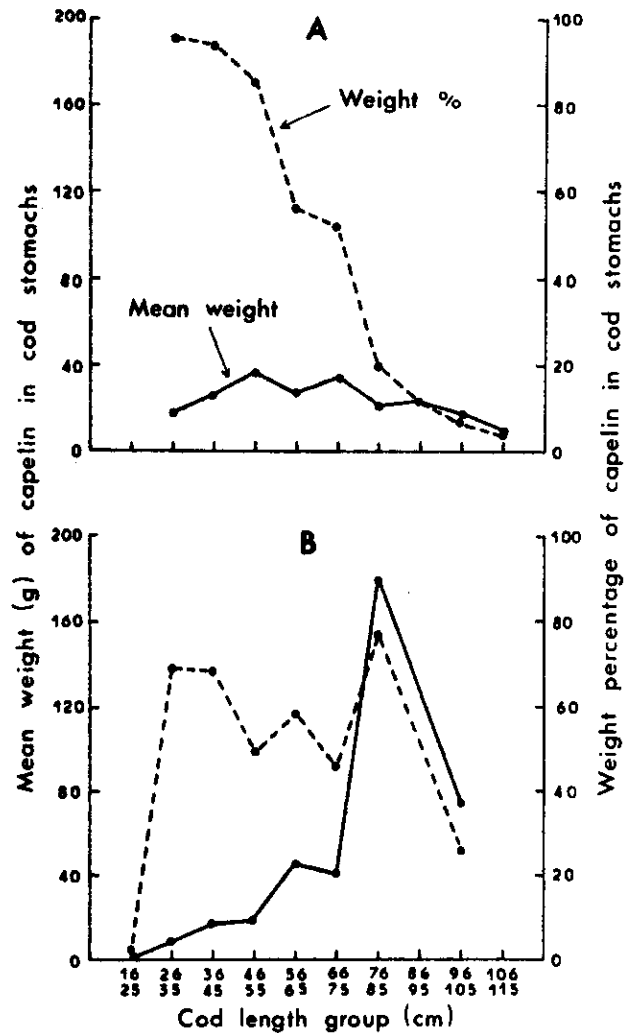


Fig. 4. Variation in predation of cod on capelin in (A) Div. 3Pn, 4R and 4S, and (B) Div. 2J, 3K and 3L.

are found on the slopes of the offshore banks in winter. In late spring and summer, cod feed intensively on capelin during and after their migrations inshore to the coasts of southern Labrador and eastern Newfoundland in one case and to the north shore of the Gulf of St. Lawrence in the other. During other periods of the year, the predation of cod on capelin is not well known but it is likely to be much less intensive. Therefore, for the purpose of calculating the annual consumption of capelin, it is assumed that they are prey for cod for about 6 months of the year.

The studies of Karpevitch and Bokoff (cited by Barrington, 1957) indicate that cod take food only when the stomach is empty and gastric digestion of the previous meal had been completed and that this process takes an average of about 5 days. Thus a cod may take about 6 meals per month or 36 meals during the periods of predation on capelin each year.

From more recent experiments on the elimination rate of food from the stomachs of three gadoid species, Jones (1974) expressed the rate of gastric digestion (r) by the relationship:

$$r(\text{g/hr}) = \frac{10^{0.035(T_o - T_c)} X^{0.46} Q L^{1.4}}{175}$$

where T_c = temperature of experiment ($^{\circ}\text{C}$),
 T_o = observed temperature ($^{\circ}\text{C}$),
 X = weight of ingested food (g),
 Q = rate of elimination of 1 g of food from the stomach of a 40 cm cod at temperature T_c , and
 L = length of cod (cm).

For a temperature $T_c = 6^{\circ}\text{C}$, the rate of digestion $Q = 0.086$

g/hr if the cod are starved prior to feeding, and $Q = 0.15$ g/hr if cod receive regular meals before the experiment.

Taking the mean lengths of cod in the research catches from Div. 2J, 3K and 3L (49.2 cm) and Div. 3Pn, 4R and 4S (50.5 cm) and the corresponding average weights of capelin ingested by an average cod in a meal (27.8 and 29.4 g), and, using $Q = 0.86$ g/hr and $T_o = 3^{\circ}\text{C}$ as representative of the natural feeding conditions of cod in the areas surveyed, the time for digesting a meal is estimated from the above equation to be 3 days. An average cod would therefore ingest about 60 meals during the periods of its annual predation on capelin.

On the basis of the assumptions made and the parameters calculated in regard to the feeding of cod, estimates of the annual consumption of capelin by an average cod in both major regions are as follows:

	36 meals per year		60 meals per year	
	2J,3K,3L	3Pn,4R,4S	2J,3K,3L	3Pn,4R,4S
Mean weight of capelin eaten in one meal (g)	27.8	29.4	27.8	29.4
Annual consumption of capelin (g)	1,001	1,058	1,668	1,764
Mean weight of average cod (g)	1,317	1,326	1,317	1,326
Proportion of prey eaten relative to cod weight	0.76	0.80	1.27	1.33

These calculations indicate that individual cod may consume from about 0.8 to 1.3 times their weight of capelin annually in each of the major regions surveyed.

Mean weight of food ingested annually

In an earlier section of this paper it was noted that, during the periods of predation considered, capelin constituted 56% of the total weight of food items consumed by cod in Div. 2J, 3K and 3L and 64% in Div. 3Pn, 4R and 4S. Using the range of estimates of annual consumption given above for each region, noting the assumption that these figures apply to predation on capelin for about 6 months of the year, and assuming that cod would feed equally well on other food items in the remaining 6 months, the annual consumption of food by an average cod is estimated to range from 3,575 to 5,957 g in Div. 2J, 3K and 3L and from 3,306 to 5,512 g in Div. 3Pn, 4R and 4S. The lower estimates, based on a gastric digestion rate of 5 days per meal, are very similar to the results of Kohler (1964), who found that a maximum of 3,025 g of food was ingested in a year by a cod (40–46 cm) feeding in a tank with herring.

Annual consumption of capelin by cod

Pinhorn and Wells (1972) calculated the annual age composition (age 4+) of the cod stock in Div. 2J, 3K and 3L for 1961–69. On the basis of the average stock composition by age for 1965–69 (i.e. just prior to the drastic reduction in stock abundance in the early 1970's) and

using appropriate mean weight-at-age data, the biomass of cod (age 4+) averaged about 2.6 million tons during a period when the catch averaged 650,000 tons. If cod consume from 0.8 to 1.3 times their body weight of capelin per year, the total quantity ingested by cod annually in Div. 2J, 3K and 3L under conditions in 1965–69 is estimated to range from 2.0 to 3.4 million tons.

In Div. 3Pn, 4R and 4S, the average annual catch during 1965–69 was 75,000 tons. On the assumption that the ratio of biomass to catch in this stock is similar to that for Div. 2J, 3K and 3L, the stock size in 1965–69 averaged about 300,000 tons, from which the quantity of capelin ingested by cod annually is estimated to range from 240,000 to 400,000 tons.

Discussion

The evidence presented above indicate that capelin represent 64% of the diet of cod in Div. 3Pn, 4R and 4S and 56% in Div. 2J, 3K and 3L during the winter and summer feeding periods. These percentages are considered to reflect the average feeding conditions for about 6 months of the year (i.e. 3 months during the summer and 3 months in the winter). Projected on an annual basis, the corresponding figures are 32% and 28%, under the assumption that no capelin are consumed during the

spring and autumn. Templeman (1964) indicated that capelin represented about 32% of the annual diet of cod in the Newfoundland area.

Although cod may feed on capelin during the spring and autumn periods, it is likely that the degree of feeding is much less than in summer and winter. Winters (1970) found that capelin in Trinity Bay, Newfoundland, were concentrated in large inactive schools near the bottom during the overwintering period of January to March. In early April these aggregations migrated to the near-surface water layer and dispersed for feeding which continued until June when the ripening capelin approached the beaches for spawning. If a similar behavioural pattern occurs on the offshore banks, it is reasonable to assume that capelin are much less available as food for cod during a 2-3 month period in the spring. The post-spawning movements of capelin are not known, but presumably they move offshore to feed, in which case they may be pelagic for 3-4 months in the autumn and thus not form a significant part of the cod diet.

On the northern Grand Bank (Div. 3L), cod feed heavily on capelin during both winter and summer (82% and 90% respectively). While both species over-winter there, mature capelin migrate in the spring and early summer towards the Avalon Peninsula and the Southeast Shoal for spawning. Many cod also migrate to these areas in early summer, but those remaining on the northern part of the Grand Bank feed on non-migrant immature capelin (Templeman, 1964). On the offshore banks of Div. 2J and 3K, however, cod feed mostly on lanternfishes during the summer with capelin comprising only 2% of their diet. A significant part of the cod stock in these divisions migrates to inshore waters of southern Labrador and northeastern Newfoundland during the summer (Templeman, 1964), when it is estimated that capelin comprise 90% of their diet during July and August (Campbell and Winters, 1973). Consequently, the average value of 56%, found in the present investigation as constituting the proportion of capelin in the diet of cod during summer and winter in Div. 2J, 3K and 3L, is undoubtedly a minimum estimate for the cod stock complex as a whole.

In Div. 3Pn, 4R and 4S, capelin are ingested in large quantities in summer (78%) and winter (59%). After overwintering off Southwest Newfoundland cod and capelin migrate northward in the spring to the northeastern part of the Gulf of St. Lawrence (Div. 4R and 4S) (Minet, MS 1976). Many of these cod migrate to coastal waters in the Strait of Belle Isle and along the Quebec coast, where no sampling was carried out but where they are presumed to feed more heavily on capelin than was found in the samples taken offshore. Consequently, the average value of 65%, representing the proportion of capelin in the diet of cod in this area, may also be under-estimated.

In the present study, it is estimated that cod may consume from 0.8 to 1.3 times their weight of capelin annually. Using a different approach, Campbell and Winters (1973) suggested that cod consume 0.5-1.0 times their weight of capelin annually. Winters and Carscadden (1978) indicated that the best empirical estimate of this range is 0.7-1.0, and used 1.0 as applicable to the consumption of capelin by cod in the Newfoundland area under conditions of rational exploitation of cod in the late 1960's. However, in view of the preceding discussion, the estimated annual consumption rates of capelin by cod (0.8-1.3) may be minimum values.

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Review of Capelin Ecology and Estimation of Surplus Yield from Predator Dynamics

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Abstract

Information on the general ecology of capelin in ICNAF Subareas 2 and 3 is reviewed. Because of declines in the stock of several major predators, it is hypothesized that there is a surplus of capelin available for exploitation by man. On the basis of feeding dynamics of cod, seals and whales, it is estimated that there are 1.25 million metric tons of capelin available annually as surplus to the maintenance of these predators. If information on Barents Sea capelin is taken as indicative of conditions in the Northwest Atlantic, variations in recruitment and spawning stock size may be considerable. It is suggested that, in the absence of data on recruitment fluctuations, the total allowable catch of capelin should not exceed 250,000 tons for the area as a whole, with partitioning into several components for better management of the resource.

Introduction

Capelin, *Mallotus villosus*, is the most important fish fodder resource in Canadian waters of the Northwest Atlantic, being preyed upon by a wide variety of fish species, mammals and seabirds (Templeman, 1967; Campbell and Winters, 1973). The commercial exploitation of capelin was relatively unimportant prior to 1971, but since that time a very significant fishery has rapidly developed. Because of the importance of capelin both as a food source for many important commercial fish species and other marine animals and also as a resource exploited commercially by man, it has been necessary to regulate the capelin fishery. Many stocks of fish and marine mammals which are capelin predators have declined in recent years, and consequently there may be an abundance of capelin which is surplus to the maintenance of these stocks of predators. This paper reviews the ecology of capelin in the Northwest Atlantic and provides estimates of the quality of surplus capelin potentially available to man.

Review of Capelin Ecology

Trends in recent catches

Commercial exploitation of capelin offshore began in

1971 (Table 1) when USSR vessels caught 750 metric tons on the Southeast Shoal of the Grand Bank (ICNAF Division 3N) (Fig. 1). Nominal catches in Subareas 2 and 3 as a whole subsequently increased from less than 3,000 tons in 1971 to 70,800 tons in 1972, 65% of which was taken by USSR trawlers prosecuting an autumn fishery in the northern part of the area (Div. 2J and 3K). A further substantial increase in catch to nearly 270,000 tons occurred in 1973, nearly half of which was taken in a summer fishery on spawning capelin on the Southeast Shoal, and the remainder in an autumn fishery in Div. 2J and 3K. The capelin fishery came under ICNAF quota regulations in 1974, with the larger part of the total allowable catch (TAC) being allocated to the southern area (Div. 3L, 3N, 3O and Subdiv. 3Ps). During April and May 1974, a new fishery was developed by USSR vessels east of the Avalon Peninsula in Div. 3L and a substantial portion of the TAC (148,000 tons) was taken prior to the normal fishery on the Southeast Shoal in June and July. Since then, there have been three major capelin fishing areas: Div. 3L in April-May, Div. 3N and 3O in June-July, and Div. 2J and 3K in the autumn.

Growth and age composition

Capelin exhibit sexual dimorphism in size, males becoming increasingly larger than females up to the age of

TABLE 1. Nominal catches of capelin (metric tons) in ICNAF Subareas 2 and 3 by stock areas, 1970-76.

Area	1970	1971	1972	1973	1974	1975	1976
2+3K	426	242	45,623	136,422	126,939	198,501	216,323
3L	2,266	870	1,241	3,876	57,713	34,097	33,809
3NO	—	750	21,417	126,875	100,751	131,783	110,291
3Ps	307	999	2,522	1,356	2,248	1,583	60
Total	2,999	2,861	70,803	268,529	287,651	365,964	360,483

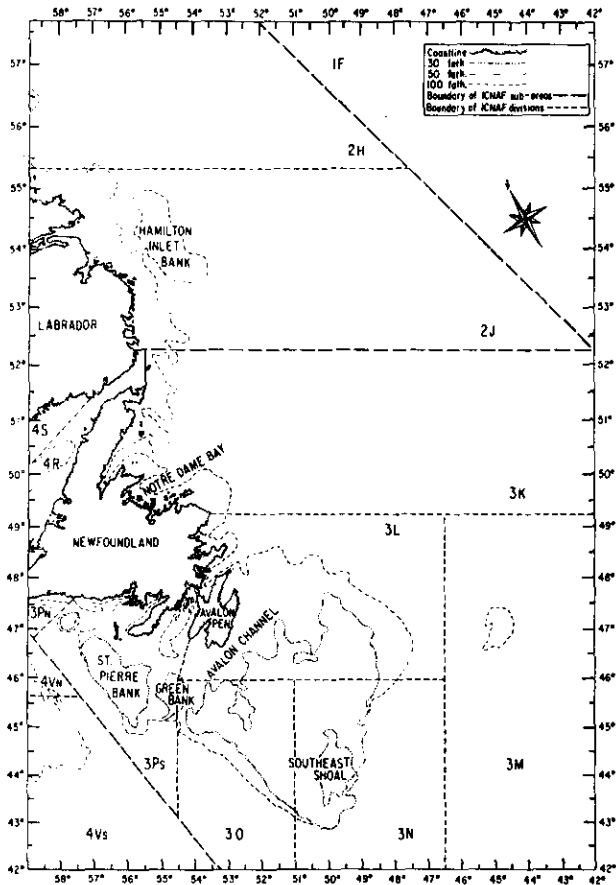


Fig. 1 Map of a portion of the Northwest Atlantic showing the ICNAF divisions and place names mentioned in the text.

maturity, after which the growth differences are maintained (Templeman, 1948; Pitt, 1958; Winters, MS 1974a). Spawning schools are normally dominated by age-groups 3 and 4, although there is considerable annual variation in growth and age composition (Winters and Campbell, MS 1974). They found significant positive correlations between temperature and size-at-age for Grand Bank capelin in 1967-73, and interpreted the fluctuations in the relative abundance of age 3 and 4 fish as reflecting growth-induced variation in maturation rate rather than variation in survival rate. In an analysis of 1967-76 data for the spawning stock on the Southeast Shoal, Carscadden (1977) found that the correlation between mean length-at-age of mature capelin in the year of spawning and mean bottom temperature 2 years previously were not significant. However, if the 1974 and 1975 data which deviated most from the trend were omitted from the analysis, the correlations became significant and positive. While Carscadden (1977) agreed with the interpretation of Winters and Campbell (MS 1974), he suggested that temperature may not be as important in determining the growth rate as previously inferred.

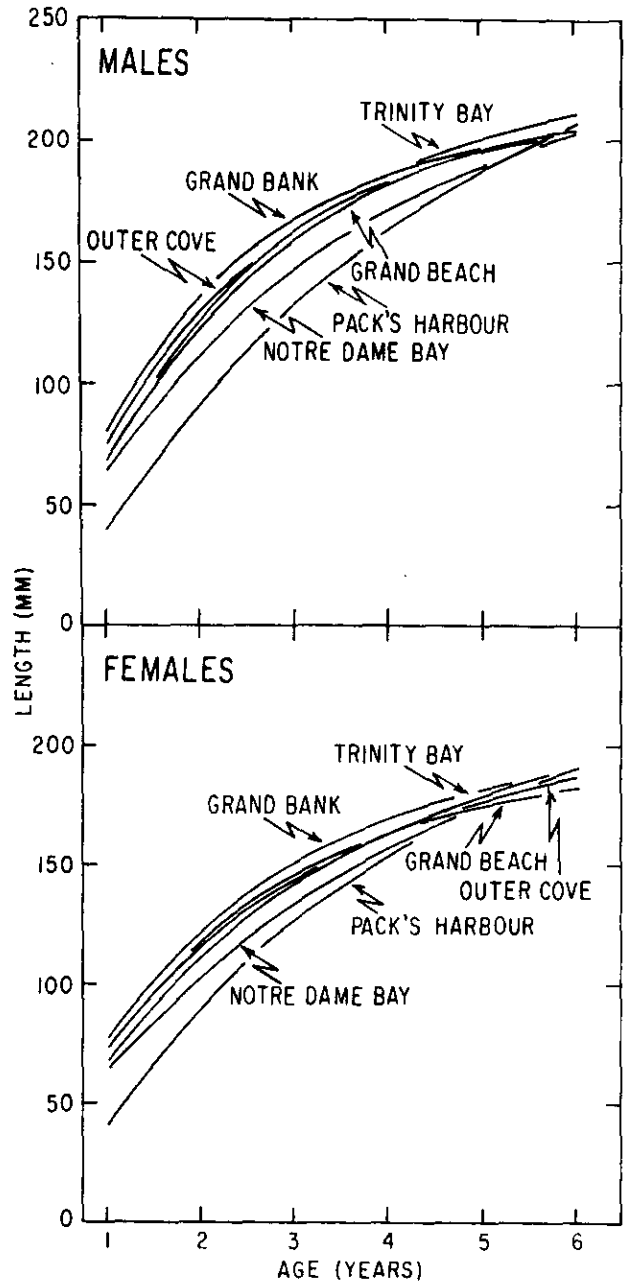


Fig. 2. Comparison of von Bertalanffy growth curves of capelin from various localities in the Labrador-Newfoundland area (from Winters, MS 1974a).

Winters (MS 1974a) showed that there is a general north-south cline in the growth of capelin (Fig. 2). Capelin from the Grand Bank and southern Newfoundland areas (Div. 3L, 3N, 3O and Subdiv. 3Ps) have a similar growth pattern and represent fish with a fast growth rate and large average length-at-age, particularly in fish younger than age 5, whereas capelin from Labrador (Div. 2J) are

characterized by fish with a relatively smaller length-at-age in the younger age-groups and a growth rate which accelerates with age to produce as large a maximum size as for capelin from the southern area. Capelin from the intermediate area (Div. 3K) have a growth rate which is intermediate between those of capelin from Labrador and the Grand Bank. The cline in growth from north to south is also reflected in the maturation rate, Labrador capelin tending to mature about 1 year later than Grand Bank capelin.

Mortality and yield

Total mortality estimates for Grand Bank capelin (Winters and Campbell, MS 1974) indicate that spawning mortality increases with age and is extremely high, particularly in males. Repeat-spawners apparently do not contribute very significantly to the spawning schools, probably being less than 20% of the population as a whole. Maximum yield-per-recruit can therefore only be achieved by generating large amounts of fishing effort which, if applied to spawning schools, will have a minimal effect on subsequent yields. Regulation of fishing mortality in relation to a specific yield-per-recruit level should not therefore be the main consideration in managing a fishery applied to spawning capelin, but the important guideline should instead be the assurance of future recruitment through adequate deposition of spawn.

Identification of capelin stocks

On the basis of seasonal distribution and probable migration patterns, Campbell and Winters (1973) suggested that the capelin resource in Subareas 2 and 3 could be partitioned into four stocks:

- a) the Labrador-Northeast Newfoundland stock, based mainly on evidence from USSR surveys during September to December 1972 (Kovalyov and Kudrin, MS 1973), which indicated that capelin in the Hamilton Bank area migrated southward in the autumn to overwinter in the Notre Dame Bay area (Div. 3K); these fish presumably spawn on inshore beaches in Div. 3K during the following summer;
- b) the Northern Grand Bank-Avalon stock, based mainly on inferences from tagged cod which migrated from the northwest part of the Grand Bank in early June to the Avalon Peninsula during the capelin spawning season in that area;
- c) the Southeast Shoal stock, which is assumed to be a separate spawning stock due to the concurrence of spawning times of inshore and Southeast Shoal capelin; and
- d) the St. Pierre-Green Bank stock, based mainly on Norwegian surveys which indicates that concentrations of mature capelin on Green Bank (Div. 3O) in May were not found there in June and presumably had moved westward to spawn on St. Pierre Bank

(Subdiv. 3Ps) or northward to spawn on beaches along the south coast of Newfoundland.

Winters (MS 1974b) showed that capelin in Div. 2J and 3K comprise different stocks with different growth characteristics but which presumably intermingle offshore during the summer and autumn in Div. 2J. He also hypothesized, on the basis of USSR (Kovalyov and Kudrin, MS 1973), Canadian (Campbell and Winters, 1973) and Norwegian (Dragesund and Monstad, MS 1973) surveys and the comparison of growth rates (Fig. 2), that the northern part of the grand Bank was a feeding and overwintering area for both inshore and Southeast Shoal spawners as well as a nursery area for immature capelin. Seliverstov and Kovalev (MS 1976) observed both mature and immature capelin in the Avalon Channel in March 1975. They also observed a southward migration of mature capelin toward the spawning grounds in Div. 3N and suggested that some mature capelin also migrate inshore to spawn.

Age compositions of mature capelin from the inshore spawning areas of Div. 3L and 3P and from the offshore area in Div. 3N are given in Table 2. Capelin spawning offshore in Div. 3N have exhibited considerable year-to-year variation in age composition and in predominance of age-classes by sex. In Div. 3P, age 3 spawners were dominant in each of the 4 years of available data. However, among the inshore spawners in Div. 3L, age 4 fish dominated in all years except 1976 when age 3 fish were the most important. The 1973 year-class has been recognized as a strong year-class (Bakanev *et al.*, MS 1976; Carscadden, MS 1976, 1977), and this is evident in the data for all three divisions noted above.

Comparison of mean length-at-age data (Table 2) indicates that differences in growth are neither large enough nor consistent enough to provide evidence of significant stock discrimination. Similar results were obtained by Winters (MS 1974a) from back-calculated data.

On the basis of the evidence presented above, it is concluded that capelin which spawn in Div. 2J and 3K are distinct from those which spawn in Div. 3L, 3N and 3P. Capelin spawning in those latter areas are also considered to be separate stocks, although there is evidence that capelin spawning inshore in Div. 3L probably mix outside the spawning season with capelin from Div. 3N. However, during the winter and spring when large concentrations of capelin are found on the Grand Bank, there is also an abundance of capelin in coastal waters. This is indicated by (a) the occurrence of capelin in the stomachs of such predators as cod, Greenland halibut, salmon and murrens taken in inshore waters; (b) mass mortalities of capelin in

TABLE 2. Percentage age composition and mean length-at-age (in parentheses) of mature capelin in June samples from Div. 3L, 3N and 3P, 1967-76.

ICNAF Div.	Year	Male					Female				
		Age 2	Age 3	Age 4	Age 5	Age 6	Age 2	Age 3	Age 4	Age 5	Age 6
3L	1967	—	21 (188)	63 (198)	15 (201)	1 (206)	—	16 (166)	19 (176)	62 (182)	—
	1969	—	20 (192)	76 (194)	4 (185)	—	—	—	—	—	—
	1972	—	5 (179)	95 (188)	—	—	—	18 (157)	75 (168)	7 (176)	—
	1973	—	3 (178)	79 (185)	18 (187)	—	—	7 (171)	67 (171)	19 (176)	2 (193)
	1974	—	24 (187)	47 (193)	29 (196)	<1 (195)	—	17 (166)	29 (177)	51 (181)	4 (184)
	1975	—	26 (187)	69 (198)	4 (200)	<1 (206)	—	15 (164)	51 (179)	23 (186)	24 (187)
	1976	—	51 (185)	48 (194)	1 (196)	—	—	45 (164)	28 (175)	20 (182)	2 ()
3N	1967	—	66 (184)	30 (191)	4 (198)	—	—	49 (166)	31 (173)	18 (179)	2 (189)
	1969	6 (164)	23 (182)	68 (193)	4 (193)	—	16 (146)	47 (159)	32 (170)	5 (184)	1 (194)
	1970	4 (166)	52 (184)	40 (189)	4 (198)	—	—	52 (165)	28 (176)	20 (182)	—
	1972	—	36 (178)	63 (185)	1 (190)	—	—	43 (158)	52 (169)	5 (183)	1 (186)
	1973	—	5 (175)	86 (179)	9 (182)	—	1 (148)	10 (158)	82 (165)	7 (173)	—
	1974	—	29 (187)	41 (193)	29 (194)	2 (192)	1 (146)	28 (166)	27 (176)	42 (179)	3 (185)
	1975	5 (168)	51 (181)	42 (194)	2 (197)	—	7 (148)	39 (163)	30 (177)	12 (185)	11 (189)
1976	—	59 (174)	37 (176)	4 (180)	1 (181)	—	72 (155)	23 (162)	4 (175)	1 (182)	
3P	1973	1 (170)	48 (174)	42 (182)	8 (185)	—	3 (144)	49 (160)	34 (170)	14 (173)	—
	1974	15 (173)	55 (185)	21 (191)	8 (195)	—	21 (160)	50 (171)	22 (178)	7 (179)	1 (187)
	1975	3 (162)	71 (187)	24 (192)	1 (190)	1 (194)	6 (139)	54 (170)	29 (180)	8 (184)	2 (197)
	1976	—	73 (184)	25 (187)	2 (192)	—	—	72 (167)	22 (177)	5 (191)	2 (191)

inshore waters during the winter (Templeman, 1948); (c) data from Canadian research and exploratory surveys (Winters, 1970); and (d) incidental catches of capelin by fishing vessels in coastal bays. Whether such coastal capelin form separate stocks from those overwintering offshore or merely represent extensions of the overwintering area is uncertain, but the evidence suggests that some mixing does occur. The migrations of cod from the northwestern part of the Grand Bank to coastal waters in June are well documented by Templeman and Fleming (1962), and it is likely that they are in pursuit of capelin migrating toward the coast. The movement of the USSR capelin fishing fleet in 1974 from the northwestern part of the Grand Bank in April to within 15 miles of the Avalon Peninsula in late May also suggests an inshore migration as well as a southward migration of the capelin schools. It therefore seems plausible to suggest that some mixing of inshore and offshore capelin occurs offshore in Div. 3L but that the proportions may vary from year to year.

Trophic relationships of capelin

The importance of capelin as a food resource for many species of fish and other animals raises the problem of how to manage the capelin fishery without undue detriment to its main predators. This is particularly true in the case of cod which, because of its abundance, size and feeding habits, is the main predator of capelin. In all areas where capelin occur, cod migrate inshore in large numbers in pursuit of capelin during their spawning migration to coastal waters (Ulltang, MS 1974; Jangaard, 1974).

Campbell and Winters (1973) estimated that capelin comprise over 90% of the diet of cod in the Newfoundland

area during June and July and nearly 32% on an annual basis. In more recent studies, Minet and Perodou (1978) found that capelin was an important component of the diet of cod in both winter and summer, averaging 64% in Subdiv. 3Pn, Div. 4R and 4S and 56% in Div. 2J, 3K and 3L.

Capelin is also the main prey species of Atlantic salmon in the Northwest Atlantic (Lear, 1972) and accounts for 45-100% of the food of salmon, depending on size, in Newfoundland coastal waters. Greenland halibut in the length range of 20-80 cm feed almost exclusively on capelin (Lear, 1969), and American plaice of 20-39 cm in Div. 3L depend on capelin for 30-38% of their food supply (Pitt, 1973). Haddock, yellowtail flounder, winter flounder, skates, sea ravens and a variety of other demersal species consume large quantities of capelin eggs and capelin during the spawning season (Pitt, 1958; Templeman, 1968). Large pelagic fish, such as bluefin tuna, also feed extensively on capelin during their summer abode in the Newfoundland area, and small pelagics, such as mackerel, also feed on capelin larvae and juveniles (Moore *et al.*, 1975).

Marine mammals also feed extensively on capelin. Mitchell (1975) found that capelin was the dominant prey species in 90% of the fin whales, *Balaenoptera physalus*, taken off northeastern Newfoundland in 1947-51 and was almost the exclusive food of fin whales in 1967-71. Sergeant (1963) reported that capelin were found in 85% of the stomachs of minke whales, *Balaenoptera acutorostrata*, caught commercially in Newfoundland waters, and that other less abundant whales, such as the sei whale, *Balaenoptera borealis*, also eat substantial

quantities of capelin.

Harp seals, *Pagophilus groenlandicus*, breed in large numbers off Labrador and northeastern Newfoundland and in the Gulf of St. Lawrence, and Sergeant (1973a) estimated that at least 25% of their diet consisted of capelin. Other species of seals (hooded, grey and harbour) are less abundant in the area but they also consume significant quantities of capelin.

Capelin form the main food supply of many seabirds in Subareas 2 and 3. Alcids, particularly thick-billed murre which overwinter along eastern Newfoundland, depend on capelin for 90% of their diet. Approximately 7 million greater shearwaters live in the Newfoundland area during the summer and depend largely on capelin for their food (Brown, personal communication). A wide variety of other less numerous seabirds, such as puffins, gannets and kittiwakes also feed on capelin.

Capelin as a Limiting Factor in the Production of its Major Predators

The biomass levels of the major predators of capelin (cod, harp seals and fin whales) have been severely reduced in the past several decades as a result of intensive exploitation. For example, the harp seal population in the Northwest Atlantic in the early 1950's was estimated to be near its asymptotic level of 3 million animals, whereas in the late 1960's intensive harvesting had reduced the population to 1.3 million animals (Sergeant, 1973a, 1973b). Similarly, the extensive international fisheries for cod which developed in Subareas 2 and 3 in the late 1950's and reached high levels of exploitation in the late 1960's reduced the cod populations to about one-half of their former levels (see later section). If food is a limiting factor in

the production and abundance of these predators, such major population changes would be expected to be reflected in such parameters as growth rate, maturation rate, fecundity, recruitment and natural mortality. Changes in these parameters are reviewed below for the three major capelin predators.

Cod

A large proportion of the annual growth of cod in the Newfoundland area occurs during the June-August period (Templeman, 1965), at which time they feed almost entirely on capelin. Consequently, the availability of capelin per unit biomass of cod should be a major factor influencing changes in cod growth. Wells and Pinhorn (MS 1970) compared Bertalanffy growth parameters of cod stocks in Subareas 2 and 3 from the early to the late 1960's and demonstrated a general increase in growth for all stocks, which they attributed to the reduction in the numbers of older fish by the commercial fishery. Data on cod growth in Div. 3K and 3L, prior to the period of heavy exploitation, have been reported by Hodder (MS 1964) for 1947-57, and estimates of population numbers at age for cod in Div. 3L back to 1955 and in Div. 2J, 3K and 3L back to 1961 have been made by Pinhorn and Wells (MS 1972). Estimates of the population size in Div. 2J, 3K and 3L back to 1955 were calculated by using the ratio of numbers-at-age in Div. 3L to those in Div. 2J, 3K and 3L for 1961-62. A comparison of population size and weight at age for cod in Div. 2J, 3K and 3L (actually Div. 3K and 3L during 1947-57) before the period of heavy exploitation (1947-62) and during the period of intensive fishing activity (1964-68) is shown in Table 3. Substantial compensatory growth increases occurred between 1947-62 and 1964-68, the differences tending to increase with age to the extent that an age 14 cod in 1964-68 was nearly 80% greater in weight than a fish of the same age in 1947-62. The increasing growth difference with age was apparently a density-dependent

TABLE 3. Comparison of age-specific weight and population size (millions of fish) for cod in Div. 2J, 3K and 3L before (1947-62) and during (1964-68) the period of heavy exploitation.

Age (yr)	Mean weight (kg)		Percentage increase in weight	Accumulative stock size (10 ⁶)		Percentage decline in stock size
	1947-62	1964-68		1955-57	1964-68	
4	0.50	0.57	14.0	2,635	1,956	25.8
5	0.75	0.94	25.3	2,183	1,278	41.5
6	1.12	1.28	14.3	1,738	770	55.7
7	1.40	1.75	25.0	1,387	459	66.9
8	1.71	2.27	32.7	1,088	259	76.2
9	1.99	2.68	34.7	702	146	79.2
10	2.14	3.13	46.3	452	86	81.0
11	2.27	3.57	57.3	254	54	78.7
12	2.39	4.06	69.9	157	36	77.1
13	2.54	4.50	77.2	107	25	76.6
14	2.69	4.81	78.8	67	17	74.6
15+	3.06	5.25	71.6	45	12	73.3
	ΔW (unweighted)		54.3	Decline in numbers		25.8
	ΔW (weighted)		26.5	Decline in biomass		34.2

response to the increased reduction in numbers of older fish relative to younger age-groups.

Relative to the population age structure in 1964-68, the mean weight of cod in Div. 2J, 3K and 3L increased by 26.5% from 1947-62 to 1964-68. However, the population biomass was 34% higher in 1955-57 than in 1964-68. Assuming that cod were able to take full advantage of the increased availability of food per unit biomass in the latter period, the decrease in biomass implies an increase in ration size per unit biomass. According to Paloheimo and Dickie (1966), gross growth efficiency (log K) decreases with increase in ration size, the relationship being such that increases in the food supply beyond a certain level will not lead to further increases in growth rate due to changes in energy conversion efficiency. Thus a decrease in log K in response to the increased ration size available per unit biomass of cod due to a reduction in biomass is probably responsible for the observed growth increase (26.5%) being less than would be expected from the reduction in stock size.

Recruitment estimates for cod (at age 4) in Div. 2J, 3K and 3L averaged 656 (range 485-907) million fish annually during 1955-60 and 658 (range 510-908) million fish during 1961-67 (pinhorn and Wells, MS 1972, MS 1974). Thus recruitment has remained relatively constant over the entire period, indicating that increases in the maturation rate and fecundity have been substantial enough to maintain population fecundity at a high level. It is possible, however, that the time lag has not been sufficiently long to allow recruitment changes to show up.

Changes in natural mortality (M) are difficult to detect, although a decrease in this parameter would be expected in response to a reduction in population size. Pinhorn (MS 1972) investigated the value of M for cod in Div. 2J by five methods which gave a range of 0.15 to 0.21. It is interesting to note that the highest value of M was derived from the average catch curve reflecting mortality for the 1954-55 period and the lowest value was obtained from the regression of fishing mortality on fishing effort for the 1961-66 period.

Seals

Available evidence on the feeding of harp seals has been summarized by Sergeant (1973a). After intensive harvesting during the 1950's and early 1960's, the maturation rate increased (Sergeant, 1966), implying an increase in growth rate (Laws, 1959). Sergeant also noted that moulting adults were in much better condition and fat thickness was greater in the late 1960's than during a decade or so earlier when population levels were high. These factors would undoubtedly have increased the maternal frequency, the survival rate of the young, and the net reproductive rate of the population as a whole.

Whales

The fin whale is also a major predator on capelin and as many as 5,000 animals have been estimated to live off the Newfoundland coast in summer (May-November) (Sergeant, personal communication). No data are available on trends in population parameters, but Sergeant noted wide annual variation in oil yield during 1947-51, whereas Mitchell (1975) found very little variation in the quantities of capelin in fin whale stomachs during 1967-71. Since fin whales were heavily exploited in 1947-51, the temporal contrast can only be explained by the lesser availability of capelin during 1947-71 when the cod and harp seal populations were at near-asymptotic population levels. It is therefore likely that similar increases in growth, maturation and net reproduction have occurred in fin whales as in harp seals.

Estimation of Surplus Yield of Capelin

The major predators of capelin (cod, seals and whales) have all suffered major reductions in population size over the past 3 decades. Data available on the magnitude of the declines and on consumption rates of capelin before and after major exploitation of the predators enable the construction of a simple deterministic model to provide some indication of the amount of capelin released by the decline in those predators and available to a fishery. The model implies that the production of capelin is independent of predator dynamics, and, in cases where actual data were lacking, assumptions were made on the basis of the limited information available.

Surplus capelin from attrition of cod biomass

On the basis of stock assessments by Pinhorn and Wells (MS 1974) and calculations of stock sizes from the Baranov catch equation, biomass estimates (000 tons) for the four cod stocks, utilizing capelin as a major component of their diet in Subareas 2 and 3, are as follows:

Stock area	Maximum sustainable yield (MSY)	Fishing mortality at MSY (F_{max})	Stock size at MSY level of fishing ¹
2G, 2H	30	0.70	85
2J, 3K, 3L	550	0.35	2,050
3N, 3O	100	0.20	600
3Ps	60	0.30	250
Total	740	—	2,985

¹ Calculated from Baranov catch equation.

The cod stock in Div. 2J, 3K and 3L is the largest of the four stocks described above, it has the longest time series of data, and it is taken as being representative of the other cod stocks in Subareas 2 and 3. Estimates of the initial (unexploited) biomass (B_0) are based on 3 methods of

calculation:

- (a) The logistic model of Shaefer (1954) predicts that B_0 is twice the stock size at the MSY level of fishing, i.e. $2 \times 2.05 = 4.1$ million tons.
- (b) The yield-per-recruit model, with growth, natural mortality and recruit parameters applicable to cod in Div. 2J, 3K and 3L, predicts that the stock size at the MSY level of fishing occurs at approximately 40% of B_0 (Gulland, 1971), i.e. $2.5 \times 2.05 = 5.1$ million tons.
- (c) From the virtual population analyses of Wells (MS 1972) and Pinhorn and Wells (MS 1972), the average stock size of cod in Div. 2J, 3K and 3L during 1955-57 was estimated to be 3.6 million tons. This is probably a minimum estimate of B_0 , as the stock actually sustained an annual catch of more than 200,000 tons during the period.

The average of the three estimates of B_0 given above is 4.27 million tons, or 2.08 times the stock size at the MSY level of fishing. Extrapolation of the average estimate of B_0 for cod in Div. 2J, 3K and 3L to include all 4 stocks mentioned above gives an overall estimate of $B_0 = 6.21$ million tons.

For a population in the equilibrium state, the production-biomass ratio (P/B) is equal to the total mortality coefficient (Z). The production (P) is defined as the product of the food intake (I) and the growth efficiency (K). Therefore, for a relatively unexploited population, we have the relationship

$$KI_0 = B_0 Z \quad \text{or} \quad I_0 = B_0 Z/K$$

Using $K = 0.1$ as the average estimate of the growth efficiency (Slobodkin, 1962), $Z = 0.2$ as the total mortality in an unexploited population, and $B_0 = 6.21$ million tons as estimated above, the total food intake (I_0) of cod at biomass level B_0 is 12.42 million tons. Campbell and Winters (1973) estimated that capelin represented 32% of the food intake of cod annually during 1947-51, from which the annual consumption of capelin (C_0) by cod at B_0 is 3.97 million tons. Thus, the annual consumption of capelin per unit weight of cod (R_0) is $3.97/6.21 = 0.64$. This value is within the range of R (0.5-1.0) indicated by Campbell and Winters (1973).

From 1955-57 to 1964-68 the reduction in the biomass of cod in Div. 2J, 3K and 3L increased the nominal availability of food per unit biomass of cod by 34% which produced a density-dependent growth increase of only 26.5%. Because of the relationship between ration size and growth efficiency, it is probable that the food consumption of cod increased more than the rate at which growth increased. It is unlikely, however, that cod were able to take

full advantage of the increased availability of capelin, since all cod do not migrate to shore in pursuit of capelin, and this is particularly so with regard to the younger cod which characterize the present age structure of the stock in the northern area. Therefore, the reduction in the cod biomass to one-half of that for B_0 through fishing is unlikely to have resulted in a doubling of R_0 . Consequently, the upper limit of the range indicated by Campbell and Winters (1973) was used, i.e. $R = 1.0$, which represents a 56% density-dependent increase over R_0 , and the annual consumption of capelin (C) is therefore estimated to correspond with the biomass of the predator at the MSY level of fishing, i.e. 3 million tons.

Assuming that the biomass level of capelin has remained relatively constant, the surplus production of capelin released by the decline in the cod stocks is 0.97 million tons.

Surplus capelin from attrition in seal population

The present population of harp seals in the Northwest Atlantic is estimated to be 1.3 million animals, whereas the population prior to the recent period of heavy exploitation was about 3.0 million animals. The asymptotic level is in all likelihood greater than 3 million animals, but, taking into account the density-dependent increase in growth, it is reasonable to assume that the present biomass (B) is about 50% of the level representative of the virgin stock (B_0).

Sergeant (1973a) estimated that 400,000 tons of capelin are consumed by harp seals at present levels of population size, of which 300,000 tons (C) are eaten off eastern Newfoundland and Labrador. Assuming that the increases in growth (26%) and consumption rate per unit biomass (56%) for cod also apply to the harp seal population, the animal consumption of capelin by seals at biomass level B_0 is given by $C_0 = C(B_0/B - 0.56) = 432,000$ tons. Therefore the surplus production of capelin released by the decline in the harp seal population is 132,000 tons.

Surplus capelin from attrition in whales

The current population of fin whales off Newfoundland is approximately 2,500 animals (Sergeant, personal communication), which is about one-half of the former level (Mitchell, 1972). From data on feeding rates (Sergeant, 1971), it is estimated that each whale consumes about 100 tons of capelin during the summer feeding period in the Newfoundland area. Thus the current consumption of capelin is about 250,000 tons. Assuming the same changes in R as occurred in cod, the consumption of capelin by fin whales prior to the period of high exploitation is estimated to have been 360,000 tons. Therefore, the surplus production of capelin released as a result of the decline in the fin whale population is 110,000 tons.

Minke whales are abundant in the Newfoundland area and depend largely on capelin for their food supply (Sergeant, 1963). Their daily consumption of capelin is estimated to be 0.13 times that for fin whales (Sergeant, personal communication), which, extrapolated to the feeding season, indicates a current consumption of about 35,000 tons of capelin. Assuming the same changes in population size and consumption rate as for fin whales, the surplus capelin released by the decline in the minke whale population is about 15,000 tons.

Surplus capelin from decline in major predators

The total excess production of capelin released by declines in the abundance of its major predators (cod, seals and whales) and available for utilization by man is estimated to be about 1.25 million tons.

Discussion and Conclusions

The above estimate of surplus production of capelin, derived from predator-prey interactions, should be interpreted only as indicative of the order of magnitude of potential capelin yield under the assumptions used in the model. The most critical of these assumptions relate to the steady-state condition concerning capelin production and to the constancy of the relative diet composition of the major predators. Insufficient data prevent a detailed evaluation of the reality of these assumptions, but the general deterioration of temperature conditions during the 1950's and 1960's (Rodewald, 1972) suggest that capelin production may be lower now than previously; this is reflected in the reduced growth rate and older age at maturity of Grand Bank capelin in recent years (Winters and Campbell, MS 1974). It is unlikely that capelin have increased in relative importance in the diet of predators. It is also unlikely that the present cod populations, characterized by relatively more younger fish than previously, have been able to take as full advantage of the increased availability of capelin per unit of cod biomass as the older cod, which have exhibited much greater growth increases (up to 80%) and which migrate to shore in greater proportions than younger fish at least in the northern area (Pinhorn, personal communication).

Density-dependent changes in growth and maturity have been demonstrated for the major capelin predators, particularly cod. The effects of over-exploitation of capelin (directly by predation of animals and man or indirectly by recruitment failure of capelin) can therefore be expected to reverse some of these changes. For cod, a decrease in growth rate will almost certainly occur with concomitant changes in maturation rate and fecundity. A significant decrease in fecundity may or may not result in recruitment loss, depending on the stock-recruitment relationship for cod. Therefore, the minimum effect on cod would be a decrease in yield-per-recruit, perhaps accompanied by an

increase in natural mortality and a decrease in recruitment. For sea mammals, similar changes in growth and maturity may be expected which would likely cause a decrease in net reproductive rate and thus in sustainable yield rate. If the capelin resource in Subareas 2 and 3 is already being fully exploited, the effects on the major predators of a commercial fishery on capelin should soon appear. For example, the Humboldt Current anchoveta population has fluctuated rather dramatically in response to environmental variations which were soon reflected in parallel changes in the predator bird populations (Shaefer, 1970); the development of an intensive and highly competitive fishery for anchovy in the late 1950's resulted almost immediately in a very significant decline in the bird populations which have since remained at relatively low levels of abundance. A second example is the Bering Sea fur seal population which depends largely on the Alaska pollock as its major prey resource. In recent years, an intensive fishery for pollock has removed most of its capital stock with the result that substantial reductions in growth, net reproductive rate and recruitment have appeared in the fur seal population (Joseph *et al.*, 1974; Sergeant, personal communication).

Although the potential yield of a capelin fishery may be large, the very large spawning mortality of capelin implies that both the stock size and the potential catch will fluctuate directly in response to recruitment variations, which may be substantial. For Barents Sea capelin, recruitment (estimated from catch-per-unit-effort data) during 1951-61 fluctuated by a factor of 17 times, the lowest estimate being only 20% of the average for the period (Gjosaeter, MS 1972). The parent stock fluctuated by a factor of 11 times over the same period, the lowest abundance estimate being 20% of the average. Information on fluctuations in biomass and recruitment of capelin in the Northwest Atlantic is scanty and no direct information is available as to the specific levels of spawning stock and recruitment required to support the capelin fishery. In the absence of such information, the total allowable catch (TAC) of capelin in Subareas 2 and 3 should not exceed the lower limit of fluctuation in spawning stock size, particularly in view of the possibility of successively poor year-class survival that may result from rather severe hydrographic conditions since 1971. Taking 1.25 million tons as one estimate of the potential sustainable yield of capelin available to man and 20% as the lower limit of fluctuations in the spawning stock, a TAC of 250,000 tons is implied.

Partitioning of the TAC of capelin by smaller management areas would be desirable. Age composition data indicate that capelin in Subdiv. 3Ps belong to a different stock from those in Div. 3L, 3N and 3O and consequently should be allocated a separate TAC. The fishery on pre-spawning capelin in Div. 3L should also be allocated a separate TAC, since this is probably an area of

mixing for capelin destined to spawn inshore and on the offshore banks. The TAC for this area should be relatively small in order to reduce the possible effect of the fishery on the inshore migration of cod and also because of the general desirability of restricting capelin fisheries to the spawning season, thus ensuring that juvenile capelin are not exploited. The stock relationships of capelin in Subarea 2 and Div. 3K are not clear, but, in order to prevent excessive exploitation of any one component of the stock complex, the TAC should be partitioned into at least two components (Subarea 2 and Div. 3K0).

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Age, Growth, Year-Class Strength, and Mortality of the Haddock, *Melanogrammus aeglefinus*, on the Southern Grand Bank and Their Relation to the Haddock Fishery of this Area

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Abstract

Nominal yearly catches of haddock in ICNAF Subarea 3 had three main peaks, at 79,000 metric tons in 1949, 104,000 tons in 1955 and 80,000 tons in 1961. After 1961, catches declined rapidly to 14,000 tons in 1963 and gradually to 1,500 tons in 1975. Especially in the early years of the haddock fishery, a large part of the catch was often discarded at sea. Large numbers of haddock migrating from the Newfoundland banks were reported in Newfoundland coastal waters at approximately 5-year intervals from 1920 to 1950, and in 1953 and 1959.

In studies of research samples of haddock from the southern Grand Bank (ICNAF Divisions 3N and 3O) in 1946-68, the more successful year-classes from 1942 to 1968 were in declining order: 1949, 1942 or 1955, 1946 or 1952, 1953 or 1956. There were no other strong year-classes between 1942 and 1968. The 1940 year-class was probably as successful as that of 1946, the 1941 year-class was of intermediate strength, and there were large year-classes in 1934-36 and 1927-29. Within the period 1940-56 when successful year-classes were produced, haddock of the most successful year-class were more than 600 times as numerous as those from the least successful year-class. Year-class success was inversely related to iceberg number. A successful year-class typically appeared about 6-7 years after the occurrence of a previously successful year-class when most of the females of the earlier year-class had become mature.

Numbers of haddock of 5-7 years of age in research catches were only 5% of those at 2-4 years of age for the unsuccessful 1958-62 year-classes, compared with 50% for year-classes 1952-56 which included two successful and two moderately successful year-classes. The increased growth of young haddock in the more recent years, especially after 1961, was a factor in producing this result and the consequence was a much greater reduction than expected in numbers of spawning females. The quantities of spawning females on the bank between 1946 and 1962 were apparently sufficient to produce successful year-classes, but from 1963 onward were greatly below the levels at which successful year-classes were produced.

The instantaneous total mortality coefficient (Z) for fully recruited ages increased gradually from 0.64 for the 1942 year-class to 1.90 and 2.29 for the 1955 and 1956 year-classes, and decreased to 1.23 and 1.14 for the 1958-59 and 1961-62 year-classes. Ages of full recruitment declined from 4 to 7 years for the 1942-56 year-classes to 3 years for the 1958-59 year-classes and to 2 years for the 1961-62 year-classes.

Length-at-age data for ages 2-12 in January-June 1946-68 showed moderate growth in the early part of the period, lower growth in the intermediate years of high abundance of young fish, and considerably higher growth in the latter part of the period as haddock become scarcer. In this latter period, haddock grew faster as soon as the numbers at or near their size and age became scarce. Female haddock grew faster than males after age 3.

Introduction

The age and growth of haddock on the Grand Bank were studied by Thompson (1939) from research vessel catches, Rojo (1959a) from samples taken at sea on Spanish trawlers, Hodder (1966) and Hodder *et al.* (MS 1970) from samples taken from the landings of Newfoundland trawlers, and by Noskov (MS 1962) and Shestov (1967, age but not growth) from catches by Russian trawlers and research vessels.

The two major populations of haddock in the Newfoundland area are, or more correctly were, those of the Grand Bank and St. Pierre Bank. Differences in growth rate, sizes at sexual maturity, otolith length *versus* fish length, year-class strength, and in winter and summer abodes show that these two populations are essentially separate (Templeman, 1953, 1972; Templeman and Squires, 1956; Templeman and Hodder, 1965a, 1965b). Green Bank and Whale Bank (located between Grand Bank and St. Pierre Bank) lack shallow areas such as those of St. Pierre Bank and of the Southeast Shoal of the Grand Bank which warm up relatively quickly and serve as feeding grounds for haddock during the summer. The usually cold water on Green and Whale banks and in the northern shallow part of the Haddock Channel between these banks (Templeman, 1975) prevents them from becoming areas of haddock abundance. Shallow-water communication along the bottom between St. Pierre Bank and Grand Bank populations is therefore limited. Younger haddock of the two populations favor shallower water than the larger fish and they are usually better separated. There is, however, probably some movement of the larger haddock from St. Pierre Bank (Subdivision 3Ps) in the deeper water along the slope to the western part of the Grand Bank (Div. 3O).

The material for this paper is based on research samples from the southern Grand Bank, Div. 3N and 3O (Fig. 1), taken in January–June 1946–68. The period spans the rise of the haddock fishery from a small fishery to maximum catch and the decline to a fishery of negligible proportions. The haddock fishery of the Newfoundland area was the first to fail. Subsequently all haddock fisheries of the Northwest Atlantic passed from high to very low catches as the stocks were overfished and as year-classes failed. In no other area, however, was the decline as complete as for the Grand Bank. The story of this population is a very good example of how a fishery can disappear while being watched carefully by fisheries biologists and an international regulatory body. As noted by Templeman (1965), major errors of judgment are possible if a calculation of yield per recruit is accepted as a basis for maximum sustained yield. In the Assessments Subcommittee Report (ICNAF, 1964) it was tentatively concluded, on the basis of yield per recruit, that in 1962–63 the yield of haddock from Div. 3N and 3O was possibly a

little below maximum sustained yield. However, from lack of successful year-classes after 1955–56, this fishery declined rapidly after 1961. There is now no possibility of studying this population on a large scale. It is therefore all the more essential that available biological data covering the developing, relatively stable, and declining years of the haddock fishery be analyzed and presented.

Materials and Methods

The materials and data for this paper were mainly collected from the operations of the Fisheries Research Board of Canada research vessels *Investigator II* and *A. T. Cameron*. Fish taken in the January–June period were used, to reduce errors due to growth in the year under consideration. By January, the haddock of the Grand Bank have entered a period of very slow or zero growth and, although the immature fish (especially the younger) usually showed new growth in June, the spawning fish usually exhibited no new growth at that time.

Codends used were double manila with a mesh size (overall new) of about 100 mm in 1946–47 and 75 mm in 1948–50. A 44-mm mesh manila codend liner or cover was used during 1951–57, a 19-mm mesh nylon liner in 1958 and a 29-mm mesh nylon liner subsequently. In the early years, some samples were taken at sea on commercial trawlers which used trawls with codends of about 70-mm mesh, internal stretched measurement wet after use.

The St. John's Station research vessel cruise tracks and fishing stations for haddock on the southern Grand Bank are shown in Fig. 1. In 1946, the haddock surveys by

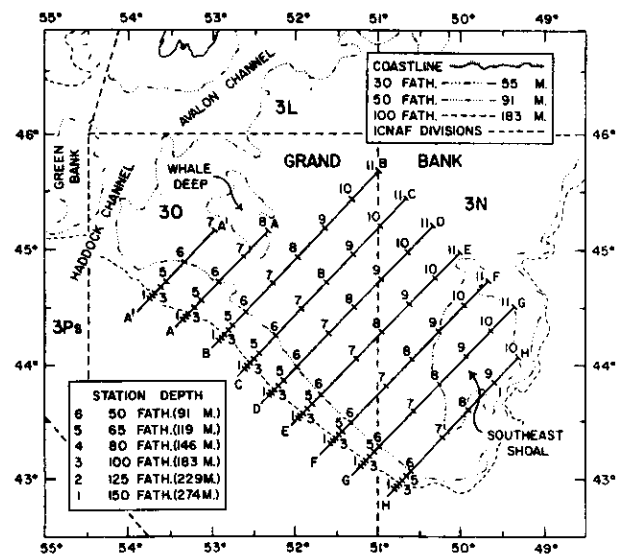


Fig. 1. St. John's Biological Station research-vessel cruise tracks and fishing stations on the Grand Bank (Div. 3N and 3O).

the *Investigator II* were at first directed toward finding areas for successful fishing. Methods of sampling and estimating catches were gradually improved. Haddock were landed and sold commercially in 1946-48 with benefits for the crew, and thus there was a bias towards repetitive fishing in areas where haddock were plentiful. In 1949 and subsequently, the catches were discarded after sampling and the development of a survey pattern began which became established in 1952 and was used in 1952-68 (Fig. 1). In some years it was possible to occupy the stations on all of the lines. In other years, only the stations on lines B, D, F and H were occupied, and occasionally during winter and early spring cruises, when most of the haddock were concentrated along the southwest slope of the bank, some of the northern stations on the bank were not occupied.

The early sampling for length and age was based on random samples of the catches. Stratified sampling for age was used later, and in recent years haddock were so scarce that entire catches were sampled. Most of the sampling was carried out at sea, but, in years when the surveys were conducted by the *Investigator II* and haddock were more plentiful, samples were also collected during the last 1 or 2 days fishing, stored in ice and examined at the Biological Station. In periods of haddock abundance, and at other times when catches were large, length frequencies were based on a random selection of the haddock caught. These random length frequencies were adjusted (from 1954 onwards) to the estimated number caught in each haul and summed to represent the length composition of the total catch. The January-June age-length key was then applied to the overall length frequency ($\%$) to obtain the age composition of the January-June survey catches. The haddock were measured to the nearest centimeter from snout to mid-fork of the caudal fin on a measuring board with the first centimeter space offset a half-centimeter from the headboard.

Scales were taken from just below the lateral line, between the second and third dorsal fins, and placed between blotting paper in envelopes. Later, the dried scales were selected for lack of regeneration and scale impressions made on a plastic slide by a roller press. The scale impressions were projected for reading ages and 1 January was taken as the birthdate. Otoliths were washed in fresh water, dried and cleaned somewhat with cloth or paper and preserved dry in envelopes. The otoliths were broken across the sulcus, mounted in black plasticine, illuminated from the side and ages read by transmitted light.

The ages of the 1946-57 samples were read by Templeman and Hodder, first from scales by Templeman, and then from otoliths by Hodder for all fish over age 6 and for 20% of those of age 6 and younger. Disagreements were resolved by examination of the scales and otoliths by both parties and agreed ages reached. In general, scales

and otoliths gave the same age up to age 6 and often to age 8 or older, but for older ages otoliths were usually more suitable. For the older fish, in cases of disagreement between scale and otolith readings, otoliths usually gave a higher reading which generally became the assigned age. Growth checks, which were commonly present in earlier years of growth, were usually more distinct and more like annual rings in otoliths than in scales. Thus, even in older fish, scale reading was often useful or even necessary to form a good opinion regarding checks in the early years in otoliths which were depended on for the later ages. Ages of the 1958-64 samples were read by Hodder from otoliths with checking by scale reading in doubtful cases. Ages of the 1965-68 samples were read by Wells from otoliths and checked by scale reading in doubtful cases, after considerable experience had been acquired in reading scales and otoliths of haddock aged previously by Templeman and Hodder.

In using the research-vessel catch per effort (successful 30-min towing on bottom) data to estimate the relative quantities of mature females and relative year-class numbers, it was necessary to make certain adjustments relative to the fishing power of the research vessels used in the surveys. In four cruises (101 paired tows of equal duration) during 1959-60, the total haddock catch (129,000 kg) of the *A. T. Cameron* (No. 41 otter trawl with 24.1-m headline) was 2.3 times that of the *Investigator II* (No. 36 otter trawl with 18.3-m headline). The *A. T. Cameron* advantage in the four cruises ranged from 1.3 to 3.5. In similar comparative fishing (56 tows) on the Scotian Shelf, the *A. T. Cameron* catch of 12,807 haddock was 1.6 times (range 1.1 to 2.1 in 2 cruises) as many as taken by the *Harengus* (No. 36 otter trawl), a vessel similar in size to the *Investigator III* (Martin *et al.*, MS 1961). A conversion factor of 0.5 was applied to the *A. T. Cameron* data for use in Fig. 6, 7 and 8. The *Investigator II* data were used for the years 1947-59 and 1963 and the *A. T. Cameron* data for the remainder, the criterion being the adequacy of the survey within the January-June period and the extent of the area surveyed. For the 1946 data, the catch per unit effort was assumed to be the same as that for 1947.

For comparisons of relative strength of year-classes, the age frequencies for each year were equated to the relative numbers at age taken per 30-min research vessel set. From the resulting data (Table 3), the relative numbers of each year-class (for Fig. 6A, B and C) were determined from the average numbers per year of age at ages 2-4, 5-7 and 2-7 respectively (but the average at 5-7 for the 1940 year-class estimated from the ratios of numbers at ages 6-7 for the 1940 and 1941 year-classes, as a proportion of average number per year at ages 5-7 in the 1941 year-class).

To calculate the relative yearly quantities of mature females on the bank, the weights of mature females were

calculated from the yearly tables of numbers per thousand at age, sex and length, as described above, and conversion factors were used to change to round fresh weight of mature females for the average numbers of haddock taken per year (January-June) per 30-min research-vessel set.

For comparison of temperature conditions with year-class numbers, average 25-m surface-bottom water-column temperatures from yearly hydrographic surveys were used. These were obtained by averaging upper and lower temperatures in each 25-m water column and then averaging for the number of 25-m columns. The locations of hydrographic stations are given in Templeman (1975). Figure 7A is derived from data for Section F (stations 16-18 at 275 m, centrally on the southwest slope of the Grand Bank, about 20 August 1952-65), and Fig. 7B from Sections D and E (stations 22-26 and 31-32 at 48-81 m, on and to the west of the Southeast Shoal, about 18 August 1951-65).

Instantaneous total mortality coefficients (Z) were obtained for the fully recruited ages, by averaging the Z values obtained from \log_e equivalents of pairs of average yearly numbers at successive ages per 30-min research-vessel set, as in Beverton and Holt (1957, p. 454) but applied within year-classes.

The mean length-at-age data, used in calculating the growth curves for the periods of years, were derived from age-length tables which were constructed by combining the random age-length frequencies (numbers per 1,000 haddock) for the individual years. Von Bertalanffy growth parameters were calculated from unweighted mean length-at-age values by the least squares method of Allen (1966).

Information on the discarding of haddock by Newfoundland commercial trawlers was derived by comparing the length frequencies of random samples measured at sea throughout the course of a voyage and random samples measured from the landings of the same trawlers at the fish plants on shore. After inspection of the sea and shore length frequencies to determine the approximate size above which no discarding was evident, a conversion factor (i.e. the ratio of the number of haddock above the greatest discard length in the sea frequency to the number above this length in the shore frequency) was applied to the number at each length group in the discard range of the shore frequency, the length frequency of discards was determined by subtraction, and the weight of discards calculated from mean weight-at-length data. The discard data for each of the years considered in Table 1 were obtained from two to four trawler trips with total catches of 200,000-600,000 haddock. Other data were obtained from the captains of three Newfoundland trawlers who at our request kept detailed logbook records of catches and discards per haul.

The nominal catches of haddock in the commercial fishery were obtained from ICNAF (1952-77).

Results

Trends in catches

Haddock catches from ICNAF Subarea 3. The nominal catches of haddock (landings converted to round fresh weight and subsequently usually referred to as catches or yields) from Subarea 3, which includes the Grand Bank and St. Pierre Bank (Fig. 2B), were insignificant before 1945, after which they increased rapidly to a first peak of 79,000 metric tons (all tons in this paper are metric tons) in 1949. Catches gradually declined to 43,000 tons in 1953, rose quickly to 104,000 tons in 1955, declined gradually to 35,000 tons in 1959, increased to 80,000 tons in 1961, declined rapidly to 14,000 tons in 1963 and gradually to 1,500 tons in 1975. The average annual nominal catch from 1948 to 1962 was 61,000 tons.

Spain took most of the haddock up to 1953. During 1954-57, Canadian and Spanish catches were

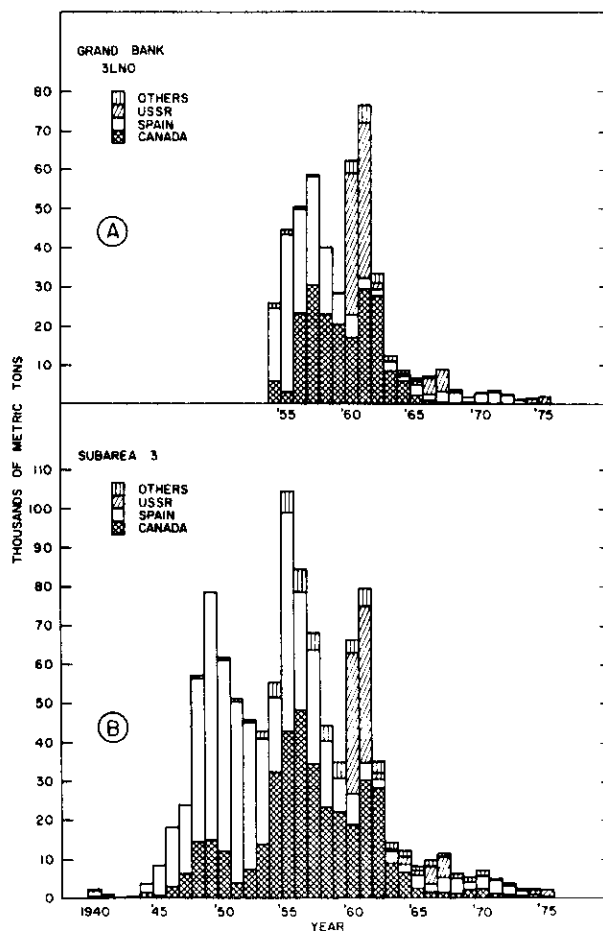


Fig. 2. Nominal yearly catches of haddock (round fresh weight) from Div. 3L, 3N and 3O and Subarea 3, 1940-75.

approximately equal, but Spanish catches declined rapidly after 1957. In 1960 and 1961, the greatest amount of haddock was taken by the USSR with Canada second in importance in the fishery. The greater part of the annual catch was taken by Canada in 1962-64 and by USSR in 1966-67. Most of the catches after 1964 were taken principally by Spain, USSR and Canada as by-catches in fisheries directed toward other species.

The haddock population forming the subject of this paper lives mainly on the Grand Bank in Div. 3L, 3N and 3O (Fig. 2A). A breakdown of catches by division was first available for 1953, but only 39% of the haddock taken in Subarea 3 were reported by division for that year. However, judging from the Newfoundland fishery, almost all the catches in 1946-52 were taken from the Grand Bank, as large catches from the very abundant 1949 year-class on St. Pierre Bank (Subdiv. 3Ps) did not begin until the autumn of 1953. Subsequently during 1954-56, even though the 1949 year-class was also abundant on the Grand Bank, only 51% of the total haddock catch in Subarea 3 was taken on the Grand Bank. From 1957 to 1962, 94% of the Subarea 3 catch was taken on the Grand Bank, declining to 77% in 1963-67 and to 53% in 1968-75. In 1954-75, 97% of haddock catches on the Grand Bank and 72% of those in Subarea 3 came from Div. 3N and 3O (40% from 3O and 30% from 3N). Ninety-four percent of the catches in the last 2 years of high yield in the haddock fishery in Subarea 3 came from Div. 3N and 3O. The haddock caught in Div. 3L form part of the Grand Bank haddock stock, mainly migrating to Div. 3L in summer from the southwestern slope of the bank and returning there in winter (Templeman and Hodder, 1965a).

Discards at sea from Newfoundland trawlers. The nominal catches of haddock (Fig. 2) are only part of the picture of haddock mortalities due to fishing. The average mesh size in the codends of Newfoundland trawlers was about 70 mm up to January-March 1957. From that time to the end of 1959 the average codend mesh size was about 100 mm, and in 1960-64 the mesh size in the codend ranged from 100 to 120 mm. Even when the codend mesh size increased, the use of chafing gear on the upper and lower parts of the codend restricted the escape of small fish.

The large discards of 31-46% in weight and 51-61% by number of haddock caught in 1949-51 (Table 1, Fig. 3) were a result of the small codend mesh and shore-plant minimum requirements for haddock of 45 cm or more in length. Because discard size at sea was by eye by individual fishermen, some haddock as much as 5 cm longer than the shore limit were discarded. Also, during this period, fish of the moderately abundant 1946 year-class were large enough to be caught but smaller than the commercially acceptable size. By 1952, haddock of

TABLE 1. Percentages of haddock catches discarded at sea by Newfoundland trawlers, 1949-60. (— indicates no data available.)

Year	Estimates by biological station observers		Estimates by trawler captains	Approximate codend mesh size ³
	Number ¹	Weight ¹	Weight ²	(mm)
1949	59	39	—	70
1950	51	31	—	70
1950	(61)	(43)	—	70
1951	—	—	46	70
1952	18	9	9	70
1953	70	45	55	70
1954	—	—	34	70
1955	—	—	21	70
1956	—	—	14	70
1957	—	—	21	70-100 ⁴
1958	1	0.4	0 ⁵	100
1959	—	—	—	100
1960	41	29	—	100-120

¹ All from Div. 3O in January-June, except percentages in parentheses from Div. 3N in July-August; see Fig. 3 for sea and shore length frequencies.

² Mainly from Grand Bank fishery but includes St. Pierre Bank.

³ Stretched mesh, wet after use; codend material was double manila in 1949-58 and manila, nylon or drylene in 1960 (Hodder *et al.*, MS 1970).

⁴ 70 mm in January-March and 100 mm in April-December.

⁵ Negligible.

marketable size were scarcer (Fig. 2) and, from the length frequencies (Fig. 3), the minimum acceptable length must have been about 40 cm, although some were evidently discarded up to 50 cm. Most of the haddock of the 1946 year-class were large enough to be retained but those of the very abundant 1949 year-class were not large enough to be caught in large numbers or were not recruited to the fishing area (Fig. 3B). Consequently, there was only a relatively small discard of 9% by weight and 18% by number. By 1953, greater numbers of the 1949 year-class were recruited to the fishing area and were large enough to be caught, but almost all were too small to be retained, and discards were as high as 45-55% in weight and 70% or more in numbers. In the following 3 years, 1954-56, haddock of the 1949 year-class grew increasingly larger and were the main objective of the fishery, haddock were landed in the round condition (Templeman and Fleming, 1958), smaller haddock became more acceptable to the plants, and discards were gradually reduced from 55% by weight (captains' estimates) in 1953 to 14% in 1956. There was a slight increase in discards to about 21% in 1957, as the abundant 1952 and the smaller 1953 year-classes entered the fishery. By 1958, however, haddock were relatively scarce (Fig. 2); the fish of 1952-53 year-classes were large enough to be acceptable to the plants; the codend mesh was larger, so that the fish of the very abundant 1955 and the smaller 1956 year-classes were not large enough to be caught (Fig. 3B); and discards were negligible. By 1960, in spite of the increasingly larger mesh

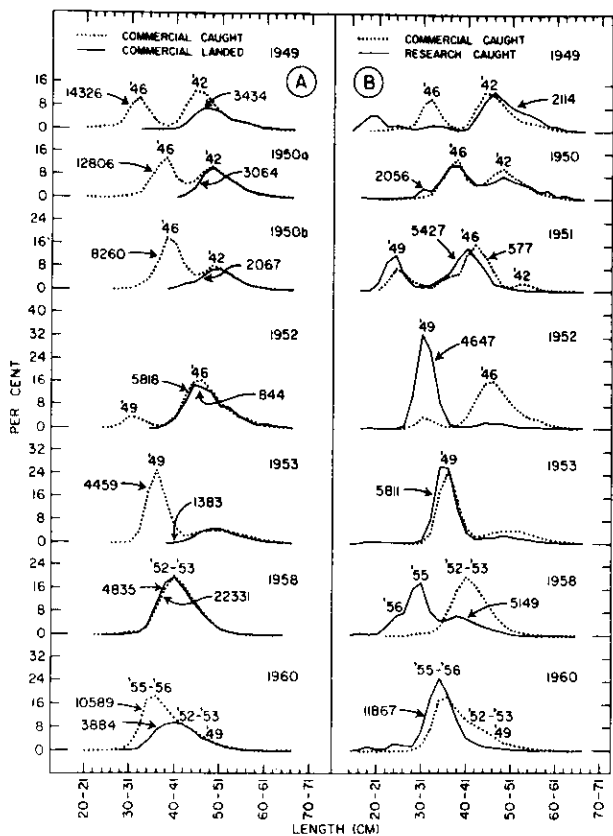


Fig. 3. (A) length frequencies of random samples of haddock measured on Newfoundland commercial trawlers at sea before discard and of shore landings from the same cruises. (B) length frequencies of random samples of haddock measured at sea on research vessels and on Newfoundland commercial trawlers. (All January-June except A, 1950b, 12 July-12 August; and B, research, 1949, 30 June-3 July. Year-classes corresponding to certain parts of the frequencies and numbers of fish measured are noted. The commercial-landed frequencies were adjusted to the commercial-caught frequencies as described in "Materials and methods". Commercial-caught frequencies in A and B are the same except 1950b and 1951.)

used, haddock of the 1955 and 1956 year-classes were large enough to be caught but had grown very slowly. Thus, discards rose again to 41% by number and 29% by weight.

Due to slight shrinkage in length between sea and shore measurements of round fish and compensating gains when measured on shore in the gutted condition (Templeman and Hodder, MS 1977), the percentages of discards calculated from sea and shore samples (Table 1) are correctly estimated for 1949-53 (measured round at sea and gutted on shore) and are slightly too low for 1958 and 1960 (measured round at sea and on shore).

Discards by Spain. Spain was one of the three countries taking large quantities of haddock from Subarea 3 (Fig. 2). During the period of significant catches of

TABLE 2. Estimates of discards of haddock by Spanish otter trawlers.

ICNAF Div.	Year	Month	% discarded (No.)	Mesh size new and dry (mm)
3N	1954	Jun-Jul	11	127 ¹
3P	1955	Mar-Apr	5	—
3O	1955	Apr	8	—
3N	1955	Jul-Aug	37	127 ¹
3N	1955	Dec	53	—
3N	1956	Sep	57	127 ¹
3N	1957	Aug	42	160 ²
3N	1957	Sep	49	130 ²

¹ Rojo (1959a); ² Rojo (1958a).

haddock, the Spanish otter trawlers and pair trawlers were producing salt fish, with cod being preferred but haddock taken when cod were not available in quantity. Fish smaller than about 40 cm were discarded (Anon., 1953; Rodriguez and Rojo, 1955; Rojo, 1958a, 1959a). Assuming knife-edge selection at 40 cm for the haddock length frequencies of Rojo (1958b, 1959b), discards of haddock by Spanish otter trawlers were calculated (Table 2). Discards on various cruises in 1954-57 ranged from 5 to 57% by number. In explaining the large numbers of discards from the ship using 160-mm mesh codends, Rojo (1958a) says that the vessel used two codend covers.

No close comparisons of Spanish and Newfoundland data are possible because only captains' estimates are available for discards by Newfoundland trawlers in the years 1954-57, but it is likely that discards by Spanish vessels were at least as high as discards by Newfoundland vessels in these years.

Research vessel catch per effort. The numbers of haddock taken by research vessels per 30-min set (Fig. 4) on the southern Grand Bank were relatively high, usually between 350 and 700 during 1947-61. In this period there were a few low points, as by the *Investigator II* in 1949 and 1950 and by the *Investigator II*, but not the *A. T. Cameron*, in 1960, which were probably due to inefficiencies in using the gear or in the chance distribution of the haddock in relation to the positions of the sets taken. It is apparent from Fig. 2 that haddock were abundant in these years, but numbers from research-vessel catches cannot be expected to match the weights of commercial catches year by year. Smaller fish were taken by the lined codend of the research trawl and hence larger numbers from a new year-class were taken in earlier years by the research than by the commercial gear. Research vessel catch per effort would have been larger in years prior to 1951, if a small-meshed codend liner had been used.

In more recent years (1963-68), consistently small numbers of haddock were taken in research vessel catches in spite of a greater than usual coverage of the

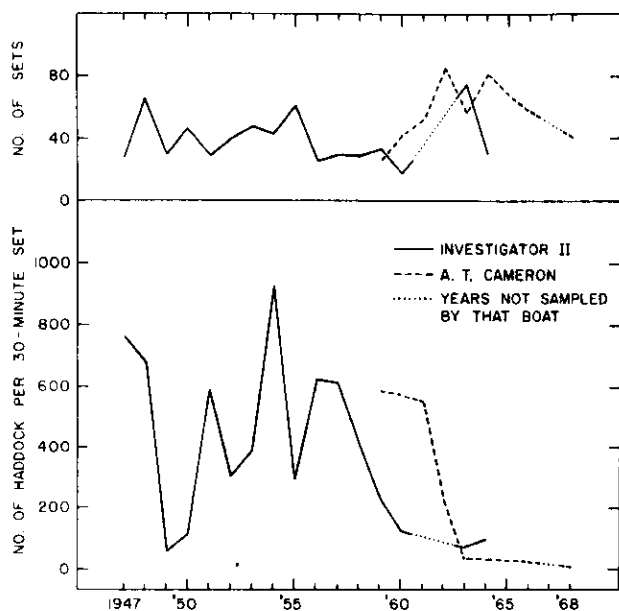


Fig. 4. Haddock catch and effort by research vessels in survey cruises for haddock on the Grand Bank (Div. 3N and 3O), 1947-68. (All January-June except *Investigator II* 1949, 30 June-3 July; and *A. T. Cameron* 1963, 12-25 July.)

area. The numbers of haddock taken per 30-min set by the *A. T. Cameron* fell from 552 in 1961 to 230 in 1962, to 33, 32, 30 and 29 in 1963-66 and to 8 in 1968. This agrees approximately in trend with the declines in commercial catches (Fig. 2), although these did not decline quite as rapidly as the research catches. After 1968, the numbers of haddock taken in research cruises on the southern Grand Bank continued to decline. In randomized groundfish surveys of Div. 3N and 3O in 1971-74 (Pinhorn and Pitt, MS 1974); Chekhova, MS 1975), the yearly average numbers of haddock per 30-min otter-trawl set on bottom ranged between 5 and 0.

Abundance in earlier years. In 1938-40, the yearly Canadian (Nova Scotian) nominal catch of round haddock from St. Pierre Bank was 2,300 tons, the USA catch 90 tons and the Canadian catch from the Grand Bank 35 tons (McKenzie, 1946). Average yearly Newfoundland haddock landings from Subarea 3 for 1929-38 were estimated at 590 tons, and USA landings from Subarea 3 from 1904 to 1920 ranged from 14 to 379 tons and from 1932 to 1940 from 3 to 194 tons (ICNAF, 1952). The highest Spanish haddock catches in Subarea 3 between 1927 and 1935 were close to 2,000 tons (ICNAF, 1954).

Although commercial landings of haddock from Subarea 3 were small before the late 1940's (Fig. 2) there are indications that haddock were abundant earlier but that they were not highly regarded by fishermen in salt-fishing for cod and were usually not recorded separately

(McKenzie, 1946). Thompson (1939) found haddock abundant on the southern Grand Bank in the early 1930's. When haddock are abundant on the Grand Bank or St. Pierre Bank, there are often in the warmer months of the year large inshore haddock migrations to the eastern part of the south coast and the southern part of the east coast of Newfoundland. Replies to a questionnaire circulated in these areas in 1950 indicated that haddock were unusually abundant in the Newfoundland inshore area at 5-year intervals from 1920 to 1950. The actual years of abundance were very likely close to the years for which they were reported. The questionnaire results, for example, gave 1920 as a year of a great inshore migration of haddock and that of 1921 evidently much smaller. However, in 1921 (not 1920, as in Thompson, 1939) the trap fishery for cod along the south and southeast coasts of Newfoundland was comparatively a failure owing to the unprecedented presence of haddock, which in some cases represented 70% of the trap catches. (Anon., 1922).

In 1953 and 1959, large quantities of haddock were observed in the inshore waters of southeastern and eastern Newfoundland. In these years most of the inshore haddock sampled in 1953 and observed in 1959 (Hodder, MS 1960) were evidently small haddock of the abundant Grand Bank 1949 and 1955-56 year-classes respectively. It is very likely that the unusual abundance of haddock inshore at approximately 5-year intervals between 1920 and 1950 represented periods of abundance on the Grand Bank and/or St. Pierre Bank and also that they ordinarily occurred a few years after the appearance of a successful year-class.

Age and length composition and variation in year-class success

Random samples from annual research surveys.

The most successful year-classes on a percentage basis (i.e. unadjusted for fishing effort and thus related in approximate relative value to only a narrow range of adjacent years) were those of 1940, 1942, 1946, 1949, 1952, 1955, 1962, 1964 and 1966 (Fig. 5). There were also successful year-classes in 1934-36, included in the 10+ age-group in the earlier years of Fig. 5.

For 1946-50, when the unlined codends retained mainly fish of age 4 and older, the percentages at these ages in the research catches (Fig. 5) are artificially increased in comparison with later years when younger fish were retained by a small-meshed codend liner or cover. Even in 1946-47 when the fishing effort was low, haddock over 60 cm in length were scarce. After 1950, relatively few were over 50 cm. The occasional very successful year-classes could often be followed in the length frequencies for 6 or 7 years. The general validity of the age readings is attested by the ability to follow the dominance of a year-class from year to year with

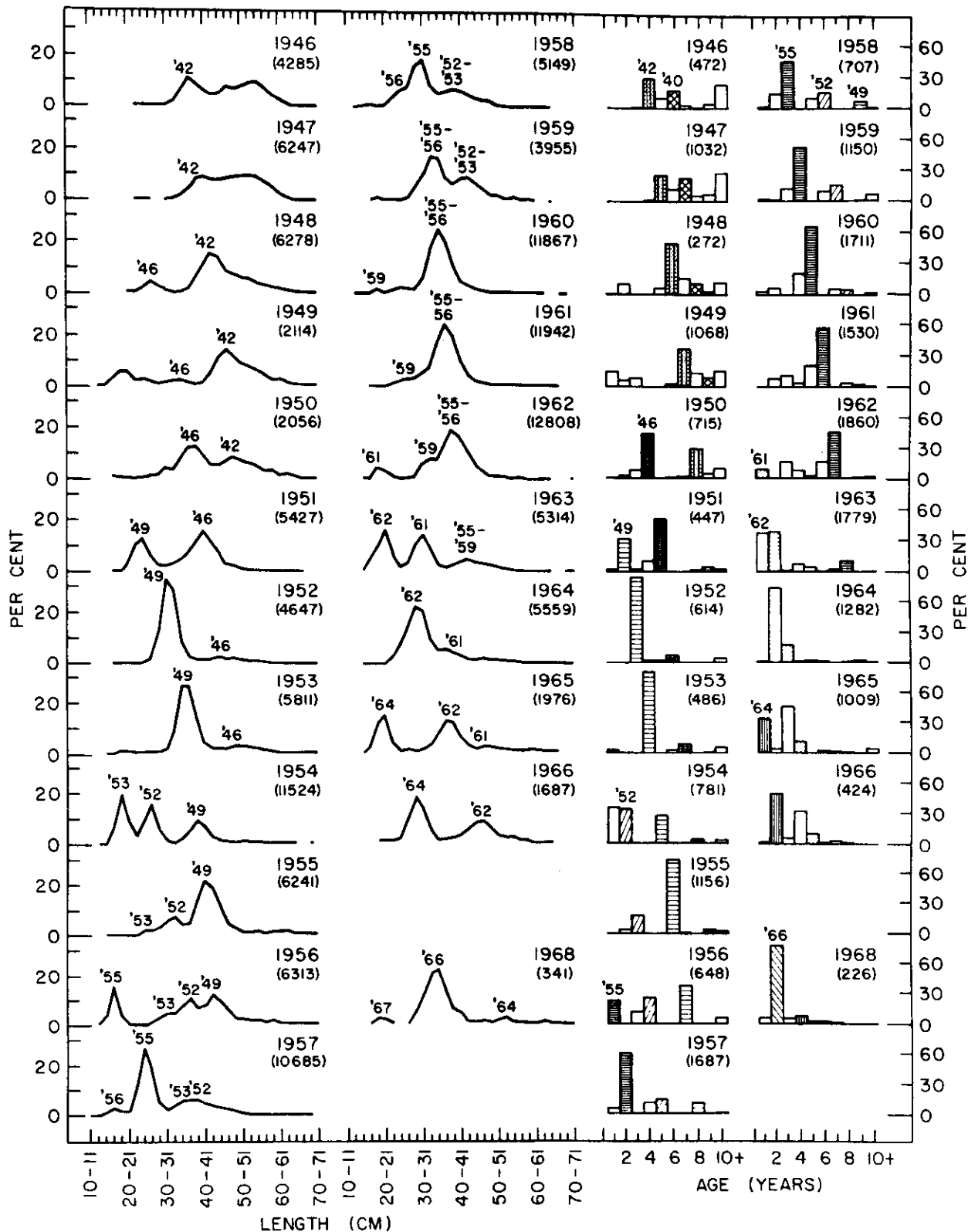


Fig. 5. Length, age and year-class frequencies from research-vessel surveys of the Grand Bank, January-June 1946-68. (Numbers measured for length frequencies and aged for age frequencies are in parentheses.)

corresponding advances in the length frequency of the year-class within the length frequency of the population (Fig. 5).

For our researches extending from 1946 to 1968, within the limits of accuracy of research-vessel catches and sampling and individual judgment, the 1942 and subsequent successful year-classes can be accepted with relative confidence as to year identity, because they were followed from young fish checked by Petersen-type frequencies (Fig. 5). Also, scale and otolith markings, differing in various years, were noted in young fish of known age and could be followed in older fish. The estimates of relative strength for year-classes before 1942 are consequently less precise because the year-classes and their scale and otolith characteristics were not identified as young fish.

Research samples adjusted to relative numbers of haddock in research survey catches. Patterns of year-class success and of some factors possibly affecting year-class success are shown in Fig. 6 and 7. The research-vessel catch-per-unit-effort, used as a base for calculations of relative year-class numbers, is imperfect because of occasional survey and gear inadequacies. The averaging of year-class numbers for 3 and 6 years reduces the variation. The relative efficiencies of the research fishing and sampling and the survival from younger to older ages are illustrated in Table 3.

It is apparent from Table 3 that the age-1 fish were not usually caught efficiently even after small-meshed codend liners were used. Numbers at age-groups 2-4 were therefore used instead of age-groups 1-4 for comparison with those at older age-groups. When the research survey was efficient in taking the younger as well as the older fish, the average numbers of haddock per set at ages 2-4 in the table should be considerably greater than at 5-7 years. The table shows that, for the 1946 year-class, age-groups 2-4 were not caught as efficiently (in 1948-50) as were age-groups 5-7 (in 1951-53). Also, the relative numbers surviving to 5-7 years of age for the 1940-42 year-classes and in a much more limited degree for the 1946 year-class should have been increased from the lack of intensive fishing for haddock before 1948. Similarly, although by 1951 the research trawl had a small-meshed codend liner, the 1949 year-class was not taken as efficiently at ages 2-4 (in 1951-53) as at ages 5-7 (in 1954-56), allowing for natural and fishing mortality. For the year-classes 1952-56 (survey years 1954-60 for age-groups 2-4 and 1957-63 for age-groups 5-7), fish of the younger age-groups were apparently taken more efficiently than in earlier years and were approximately twice as numerous as the older age-groups. The increase in fishing intensity in 1960-61 might have been expected to reduce the numbers at ages 5-7 in the survey samples for the 1955 and 1956 year-classes, relative to earlier year-classes, but there is little change in

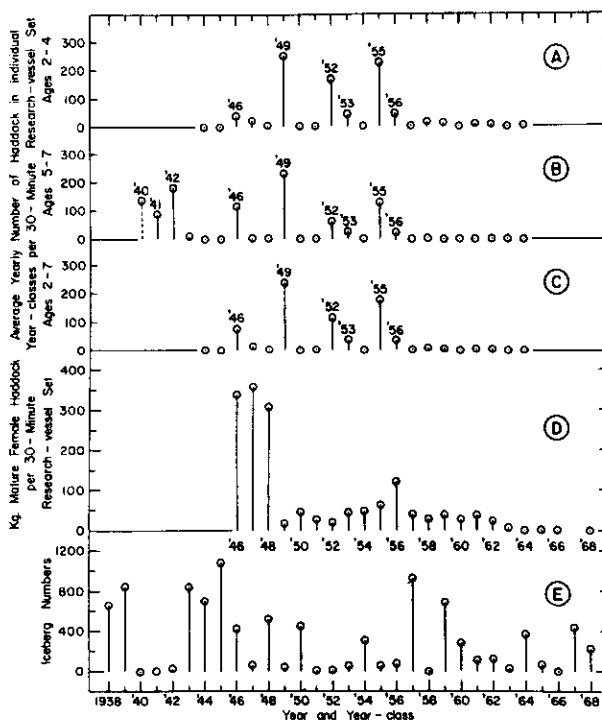


Fig. 6. Relation of relative year-class abundance of haddock on the Grand Bank to relative strength of spawning stock and iceberg numbers. [Iceberg numbers = yearly iceberg numbers south of 48°N off Newfoundland (Murray, 1969). For further information see "Materials and methods".]

the ratio of numbers at ages 5-7 to those at ages 2-4. The 1955 year-class was not fully recruited to the fishery until age 7 and the 1956 year-class until age 6 (Fig. 8). After 1956 no large year-classes appeared at any age, but haddock were relatively less numerous at ages 5-7, relative to numbers at ages 2-4, than they had been previously. For the unsuccessful 1958-62 year-classes (survey years 1960-66 for age-groups 2-4 and 1963-69 for age-groups 5-7) the ratios of numbers surviving to 5-7 years from 2 to 4 years were reduced by one order of magnitude from those for year-classes 1952-56 (averages 0.50 for 1952-56 and 0.05 for 1958-62). The decline in this ratio occurred gradually from the 1956 to the 1958 year-class, when it settled into the low survival pattern of the 1958-62 year-classes.

If all age-groups older than age 4 (i.e. 5 to 7+) are considered, the total survival after age 4 is only a little higher than for ages 5-7, the difference declining from the 1946 to the 1955 year-class and being of almost no importance afterward, i.e. from the survey year 1963 onward. The argument regarding the relationship of numbers at 2-4 years to those at later years for the periods 1952-56 and 1958-62 is unchanged by adding the numbers at ages greater than 7.

TABLE 3. Relative numbers of haddock per 30-min research vessel set in 1946-68 by groups of ages of the 1932-66 year-classes.

Year-class	Number per 30-min set				Ratios		Remarks
	Ages 1-4	Ages 2-4	Ages 5-7	Ages 5-7+	5-7 / 2-4	5-7+ / 2-4	
1932	—	—	—	8	—	—	Ages 14 and older
1933	—	—	—	12	—	—	Ages 13 and older
1934	—	—	—	87	—	—	Ages 12 and older
1935	—	—	—	128	—	—	Ages 11 and older
1936	—	—	—	250	—	—	Ages 10 and older
1937	—	—	—	107	—	—	Ages 9 and older
1938	—	—	—	62	—	—	Ages 8 and older
1939	—	—	—	92	—	—	Ages 7 and older
1940	—	—	300	378	—	—	Ages 6 and older
1941	—	—	267	286	—	—	
1942	—	222 ¹	545	644	—	—	
1943	—	10 ²	34	41	—	—	
1944	—	0.5	1.1	3.4	2.2	6.8	
1945	1.7	1.6	2.5	6.6	1.6	4.1	
1946	116	116	355	414	3.1	3.6	
1947	68	68	14	19	0.2	0.3	
1948	27	19	12	16	0.6	0.8	
1949	752	751	691	810	0.9	1.1	
1950-51	20	12	6.4	9.1	0.5	0.8	
1952	521	513	189	204	0.4	0.4	
1953	453	136	80	89	0.6	0.7	
1954	3.8	3.4	2.0	2.2	0.6	0.6	
1955	820	685	393	401	0.6	0.6	
1956	175	145	76	76	0.5	0.5	
1957	16	9.5	2.0	2.1	0.2	0.2	
1958	54	50	3.7	3.8	0.07	0.08	
1959	49	42	1.2	1.3 ³	0.03	0.03	
1960	1.8	1.7	0.2	0.2 ³	0.12	0.12	
1961	42	32	1.8 ⁴	1.9 ³	0.06	0.06	
1962	51	24	0.6 ⁵	0.6 ³	0.03	0.03	
1963	1.1	1.0	—	—	—	—	
1964	14	9.5	—	—	—	—	
1965	1.5 ⁶	1.0 ⁶	—	—	—	—	
1966	—	5.0 ⁷	—	—	—	—	
1952-56	1,973	1,482	740	772	0.50	0.52	
1958-62	198	150	8	8	0.05	0.05	

¹ Age 4 only; ² Ages 3 and 4 only; ³ Ages 7+ estimated; ⁴ Age 6 estimated; ⁵ Ages 5 and 7 estimated; ⁶ Age 4 estimated; ⁷ Ages 3 and 4 estimated.

Not only were the numbers at ages 5-7 very low compared with those at ages 2-4 for the 1958-62 year-classes, but also, within ages 5-7, the numbers at ages 6 and 7 relative to those at age 5 were low for the poorer recent year-classes. From a total of 371 haddock per 30-min set at age 5 of the 1952-56 year-classes, the numbers at ages 6 and 7 were 72 and 27% of those at age 5, whereas for the 1958-62 year-classes, from a total of six haddock per 30-min set at age 5 only 26 and 9% remained at ages 6 and 7.

Considering all the modifying factors of the foregoing, during the period of our researches (1946-68) and omitting years prior to 1946 for which complete comparisons are not available (Fig. 6, Table 3), it is probable that the most successful year-classes, based on numbers of haddock per 30-min set, were in declining order: 1949, 1955, 1946 or 1952, 1953 or 1956. The 1942 year-class was probably as successful as that of 1955, the 1940 year-class a little less

successful and the 1941 year-class was of intermediate strength. There were also successful year-classes in 1934-36. Thompson (1939) reported that the 1928 year-class was very successful on the Grand Bank. Judging by Thompson's age frequencies, the 1927 and 1929 year-classes were also successful, being more than half as numerous as the 1928 year-class. He also said that the 1933 year-class was numerous but this is not evident from his age frequencies, which show the 1933 year-class more numerous than the unsuccessful 1930-32 year-classes but considerably less numerous than the 1927 and 1929 year-classes.

There are additionally year-classes (1947, 1958, 1959, 1961, 1962) which show some strength as age 2-4 fish relative to their period and to the least successful year-classes, but, as older fish, are lacking in numbers and would be called poor year-classes. The 1947 year-class, which had a relatively low survival rate for its period, was

important in only 1 year (1951) at age 4 when 68% of the total haddock of the year-class at ages 2-7 were taken. In the other 5 years, this year-class was unsuccessful. The other four year-classes mentioned above occurred in a period of greatly increased mortality at the younger ages. The 1964 and 1966 year-classes, important on a percentage basis (Fig. 5), were relatively scarce on a per set basis (Table 3, Fig. 6).

Evidence from abundance of spawning females.

The relative quantities of mature female haddock caught during research surveys in January to June (usually May and June) of different years should be related to the relative quantities spawning (mainly in May-July), as egg numbers are correlated with the weight of the egg-bearing female haddock (Hodder, 1963). Average catches of mature females on the bank, per 30-min research vessel otter-trawl set (Fig. 6D) for 1946-62, show no close relationship with the relative success of year-classes. Throughout the period 1946-56, there were evidently adequate quantities of mature females on the bank for year-class success (because the lowest quantities, 1949 and 1952, produced successful year-classes), if other factors such as those described in Templeman (1972) were suitable. The relative weight of mature females, however, shown for 1949 may be too low since the survey was later than usual (30 June-3 July). From 1957 to 1962, the quantities of mature spawning females were similarly sufficient for year-class success but no commercially successful year-classes appeared. From 1963 to 1968 and to the present time, the quantities of spawning females were greatly below any former known levels at which commercially successful year-classes appeared.

Evidence from iceberg numbers. In 1940-58, a period covering the production of all the good and moderately successful year-classes, for which suitable data are available and age-reading is relatively accurate, and when the quantities of spawning haddock were apparently suitable for the production of successful year-classes, the year-class picture in relation to iceberg numbers (Fig. 6) is as follows:

Year-class designation	Number of icebergs		Total
	Low (<100)	High (>300)	
Good + moderate	8	1	9
Poor	3	7	10
Total	11	8	19

The good and moderate year-class-success category includes average numbers of haddock per year of age at ages 5-7, per 30-min research vessel set (Fig. 6), of from 25 to 230 fish (average 111) for the years 1940-42, 1946, 1949, 1952, 1953, 1955, 1956). The poor year-class category includes all the remaining 10 years of the period

with average numbers per set at 5-7 years of age as above ranging from 0.4 to 11 (average 3). The low-iceberg-number category ranged from 1 to 80 (average 33) and the high-iceberg-number category from 312 to 1,083 (average 659). Treated by Fisher's exact method (Zar, 1974), P (for the two-tailed null hypothesis) is 0.02, so that the relationship of good and moderate year-classes to low iceberg numbers for the 1940-58 period is considered significant.

Evidence from temperature conditions.

Average surface to bottom water temperatures (averages of 25-m water columns) are available for August of the years 1951 to 1965 for stations in the haddock area of the southern Grand Bank (Fig. 7). The deeper stations (Fig. 7A) are close to the winter and early spring abode of haddock, and the shallower stations (Fig. 7B) are in the vicinity of the late

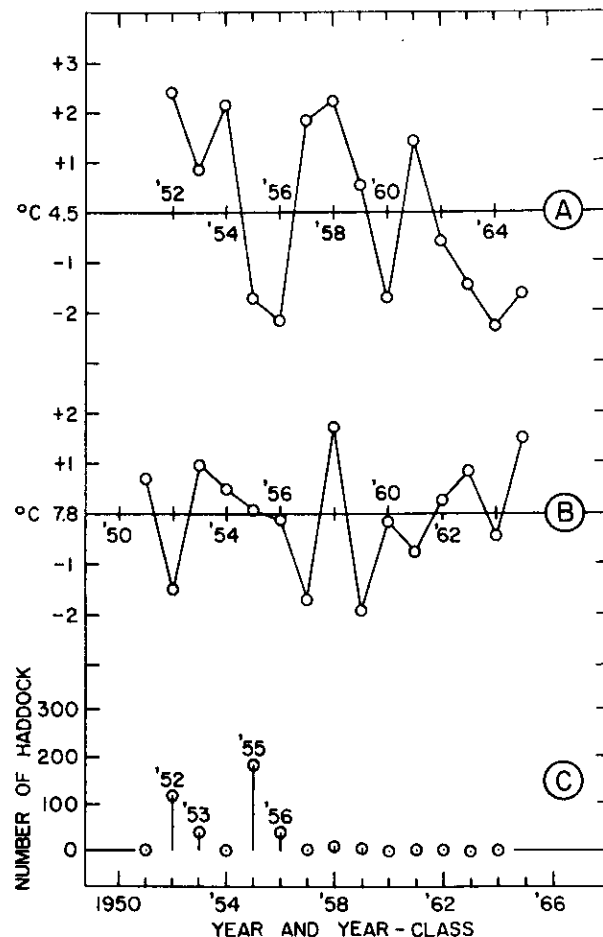


Fig. 7. Relation of temperature conditions (anomalies from averages of 25-m water-column temperatures, surface to bottom, in August) to year-class abundance of haddock on the Grand Bank: (A) temperatures southwest slope of Grand Bank (Div. 30), 0-275 m; (B) temperatures southern Grand Bank (Div. 3N and 3O), 0-81 m; (C) relative year-class numbers of haddock per 30-min research vessel set, Div. 3N and 3O, yearly averages for ages 2-7. (For further details, see "Materials and methods".)

spring and summer abodes (Templeman and Hodder, 1965a). Since these stations were occupied about a month after major spawning had ended, the temperatures should be indicative of conditions during the early larval stages. It would not be expected that water temperatures taken once a year at slightly varying dates at a station or group of stations would reflect very precisely the year-to-year temperature conditions on the bank, due to temporary changes in temperature-at-depth caused by internal waves or other abiotic factors, but such temporary changes in temperature should usually be balanced out somewhat by the averaging of temperatures taken at a number of stations over several days. However, there is no consistent relationship between temperatures in the various years and the success of haddock year-classes (Fig. 7). Some good year-classes correspond to higher and some to lower temperatures.

Total mortality

Year-class success was so highly variable for haddock of the southern Grand Bank that catch curves, based on numbers at age from the spring surveys, were not useful for estimating mortality rates. However, the numbers per 30-min research-vessel set, taken over the entire study

period, provided comparative data for estimates of total mortality (Z) within year-classes (Fig. 8).

Total mortality for the fully-recruited ages was low (0.64) for the 1942 year-class, increased to 0.83 for the 1946 year-class and to very high values of 1.90 and 2.29 for the 1955 and 1956 year-classes, and decreased to 1.23 and 1.14 for the 1958-59 and 1961-62 year-classes (Fig. 8).

There was an increase in mortality beginning at age 12 in 1961 for the 1949 year-class, at age 9 for 1961 for the 1952 year-class, and at age 8 in 1961 for the 1953 year-class. For the 1955 and 1956 year-classes, the increase in mortality began in 1961 at ages 6 and 5 respectively and was accentuated in 1962 at ages 7 and 6. The increase in Z was not so great when it began at ages 12 and 9 for the 1949 and 1952 year-classes, but was greater when it began at age 8 for the 1953 year-class and still greater beginning at ages 7 and 6 for the 1955 and 1956 year-classes. The apparent age at full recruitment to the research-vessel fishery declined from ages 4-7 for the 1942-56 year-classes to age 3 for the 1958-59 year-classes and to age 2 for the 1961-62 year-classes.

Growth

Trends in length-at-age from year to year. Length-at-age for age-groups 2-12 during 1946-68 (Fig. 9) changed gradually from a pattern of a moderate growth rate in the early part of the period to a lower growth rate in the intermediate years and to a relatively high growth rate in the latter part of the period. In the more recent years, haddock were so scarce at the greater ages that adequate numbers were not available for use in Fig. 9.

A complete series for the age-1 fish was not available because of the lack of small-meshed liner in the codend prior to 1951. For this reason, also, there was some codend selection leading to larger sizes retained for this early period. This selection should decline with age. However, even at ages up to 12 years there was a decline in length-at-age from the early to the intermediate years of the period so that the decline was real.

Because the lengths-at-age (Fig. 9) are those of January-June, the immature fish had usually not added much new growth and the mature spawning fish had usually not begun to put on new growth. The length attained during the sampling period was, therefore, usually close to that attained at the end of the previous year.

For young fish, there was a general trend for the shortest average length-at-age to be later with increasing age: from 1956 to 1958 for age 1, 1959 for age 2, 1960 for ages 3 and 4, 1961 for ages 5 and 6, and 1961 or 1962 for ages 7-9. At greater ages, suitable data were often missing but the shortest length-at-age occurred before 1962, 1963, 1964 for ages 10, 11 and 12 respectively. These results at

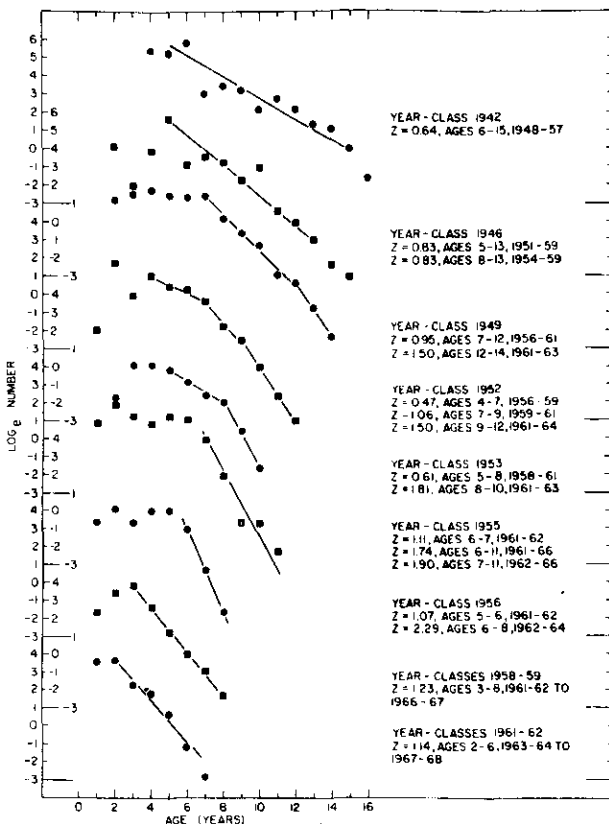


Fig. 8. Estimates of the instantaneous total mortality coefficient (Z), for relatively successful year-classes of haddock from 1942 to 1962, from catch curves of haddock per 30-min research-vessel set on the southern Grand Bank.

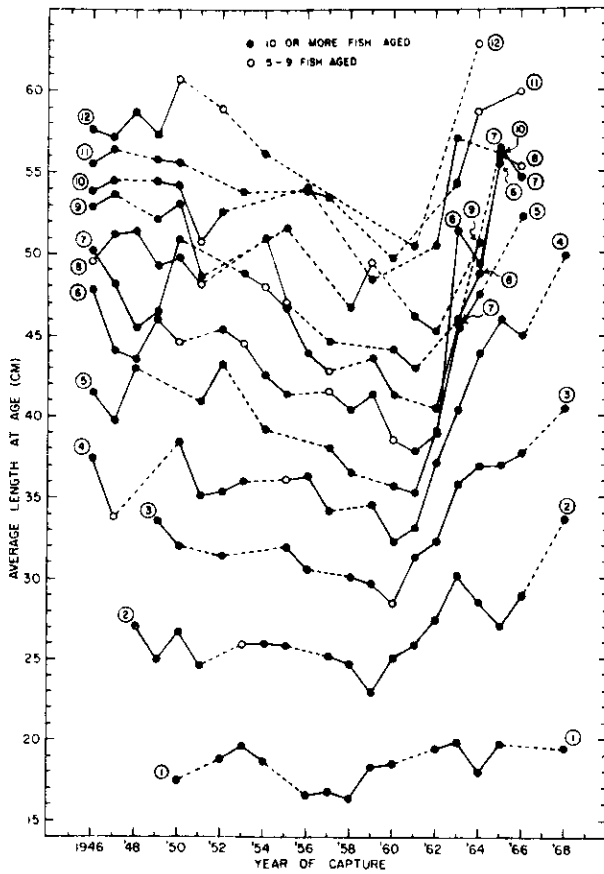


Fig. 9. Average lengths of haddock at ages 1-12 from the Grand Bank in January-June of individual years from 1946 to 1968. (For numbers aged, and relative numbers at the various ages, see Fig. 5. Broken lines are extrapolated across years in which fewer than 5 fish of the age-group were aged.)

each age from 2 to 6 (or 2 to 7) reflected the cumulative effects of slow growth on one of the 1955-57 year-classes. At greater ages, the greatest cumulative effects of slow growth were found in earlier year-classes.

Length-at-age for young fish beyond age 1 was much greater in the late 1960's than in the previous high-growth-rate period of the 1940's. The age-2 fish in 1968 were as large as age-3 fish in 1949 and the age-4 fish in 1968 almost as large as those of age 7 in 1950 and 1946.

Patterns of year-class growth. Some of the year-classes were relatively so successful as to be well represented in the samples and thus provide excellent length-at-age data for fish of the same year-class for many years (Fig. 10). At the greatest ages, the pattern was sometimes highly variable because of small numbers of fish. Apart from the variability at the greatest ages, the 1942 and 1946 year-classes and the early part of all year-classes up to 1956 showed the typical pattern of fish growth. However, beginning in 1962 and usually

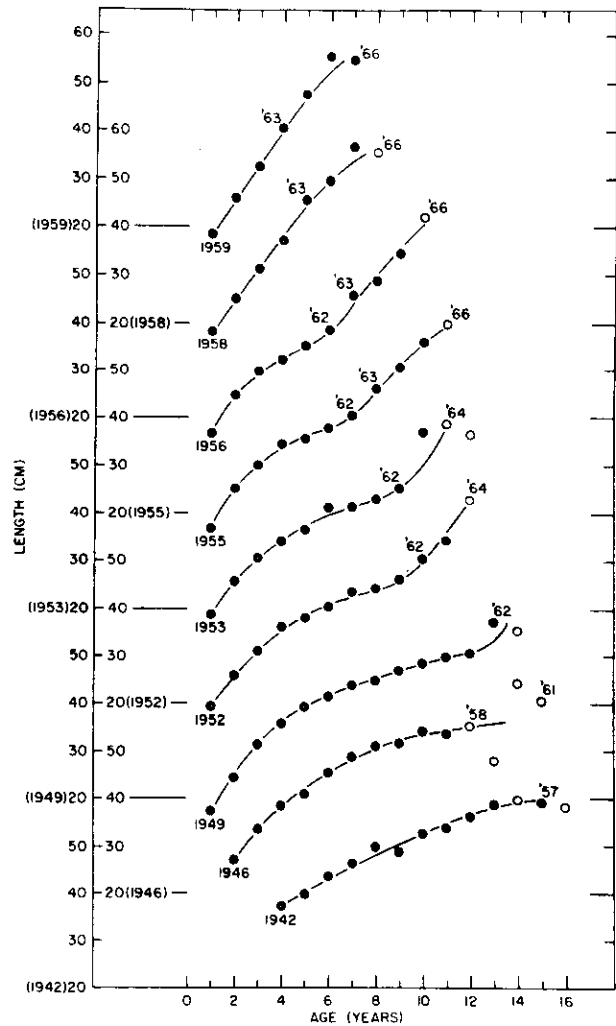


Fig. 10. Average length-at-age (January-June) of haddock from the Grand Bank, for the relatively successful year-classes of 1942 to 1956 and also for the 1958 and 1959 year-classes. (Open circles represent less than 10 fish aged. See Fig. 5 for numbers of fish aged.)

accentuated in 1963 and continuing to the limits of the data in 1966, an unusual new stanza of increased growth was apparent. The departure from the previous trend of a declining growth rate renders these curves unsuitable for a complete description by von Bertalanffy growth equations, although these could be calculated for the lower parts of the curves. The 1958 and 1959 year-classes (which were relatively unsuccessful) were growing fast enough in 1961-63 that the reduction in upward trend occurred at ages beyond the usual 3-5 years (Fig. 10, 13A).

Period growth. In view of the variation in the mean length-at-age data during 1946-68 (Fig. 9), von Bertalanffy growth curves were fitted to the data for several groups of years (Fig. 11, 13). Weighted curves were initially

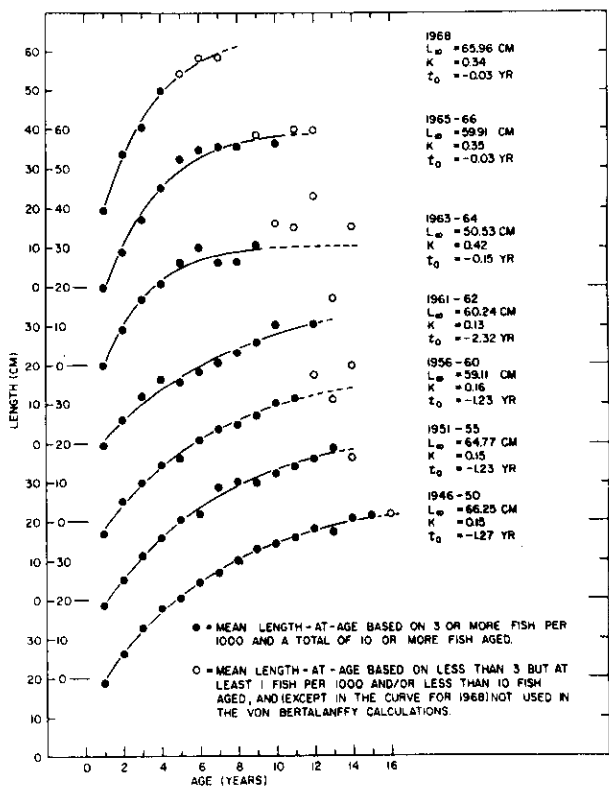


Fig. 11. Average length-at-age of haddock from the Grand Bank (January-June) for various groups of years from 1946 to 1968. fitted with von Bertalanffy growth curves. (See Fig. 5 for numbers of fish aged.)

calculated, but these were not directly comparable over the age range of the available data on account of the great variation in numbers-at-age for the various curves. For example, the weighted curve for 1946-50 data is based on significant numbers of fish at each age up to 12, whereas the weighted curves for the periods after 1960 are determined largely by the numbers of fish for age-groups 1 to 4. Consequently, the curves of Fig. 11 were calculated from unweighted mean length-at-age data for cases of three or more fish per thousand and at least 10 actually aged for the period. (Exceptionally for the 1968 curve, all points were used even though for ages 5-7 the numbers aged were 6, 5, 3 respectively.)

The most representative curves are those for the 1946-50, 1951-55 and 1956-60 periods when the haddock stock consisted of several moderate to good year-classes. There was a gradual decline in growth during those periods as indicated by the decrease in L_{∞} from 66.3 cm for 1946-50 to 59.1 cm for 1956-60, but there was little change in the growth coefficient K (0.15 - 0.16) or in t_0 (-1.27 to -1.23 years). The lowest value of L_{∞} (50.5 cm) was obtained for the 1963-64 curve, with a corresponding increase in K and decrease in t_0 . This change in the

curve is due to an increase in growth of age-groups 1-6 of the comparatively scarce haddock of the 1957-63 year-classes and the slow growth of age-groups 7-9 which were mainly fish of the numerous and slow-growing 1955-56 year-classes. The relatively fast growth of the younger age-groups and the relatively slower growth of age-groups 7-9 produced a high K and low L_{∞} . Age-groups 10-14, which were faster growing, were not used in the calculations because of their scarcity. Their inclusion would have produced a lower K and a considerably higher L_{∞} . Except for age-groups 7-9, the fish of the 1963-64 period were relatively fast growing. After 1962, there was a rapid increase in growth of nearly all age-groups present in the stock and L_{∞} increased to 59.9 cm in 1965-66 and to 66.0 cm by 1968. The fast growth of the earlier years and the slowing of growth as fish matured produced high K values (0.34-0.35) for the curves of 1965-66 and 1968. The growth rates for the younger ages were increasingly greater from 1963-64 to 1968 (Fig. 13B).

Most of the mean length-at-age values for the older fish of the 1956-60 to 1965-66 periods were greater than those represented by the curves. The older fish were so scarce that, under the conditions imposed, they were often not included in the calculations for the von Bertalanffy curves. However, the consistency of their pattern of faster growth (Fig. 11), especially in 1963-64, was great enough to indicate with certainty that the increased growth at the greater ages was real. The same consistent pattern of increasing growth in the older fish is seen in Fig. 10 for the 1949-56 year-classes. Fish older than age 10 were very scarce in the 1965-66 samples and no fish older than age 7 were present in the 1968 sample. The growth rate for 1968 was still more rapid at all ages above 1 year. The rapid increase in growth exhibited after 1961-62 pertains more to the older age-groups than to age-1 fish (Table 4).

TABLE 4. Mean length-at-age (actual) of haddock of the southern Grand Bank (Div. 3N and 3O) from 1946-62 to 1968.

	Mean length-at-age (cm)					
	1	2	3	4	5	6
1946-62	18.1	25.2	31.1	35.9	38.3	41.5
1963-64	19.8	29.1	36.8	40.7	46.1	49.9
1965-66	19.7	28.8	37.0	45.2	52.3	54.6
1968	19.4	33.6	40.4	49.9	54.4	58.6
% increase from 1946-62 to 1968	7	33	30	39	42	41

Growth of males and females. Growth curves (unweighted for the reasons given in the preceding section) were calculated from the mean length-at-age data for male and female haddock separately (Fig. 12, 13C and D). Age-group 1 was not used in the calculations, as, from

the much larger number of recorded age 1 males than females, it seemed probable that the gonads of many of the females examined had not differentiated to the point where the sex could be readily determined in a field examination. This problem was also noted by Sorokin (1957) for juvenile cod. Also, only age-groups which passed the criteria for each sex, of at least 3 fish per 1,000 and 10 fish whose ages were read for the period, were used for the von Bertalanffy calculations (Fig. 12). For 1963-64, the curve for males did not converge and no von Bertalanffy calculations could be made. For later periods, there were few sexually mature females in the samples. After age 3, the annual growth increments for females were progressively greater than those for males, with the result that the L_{∞} values for females were greater and the K values usually smaller. The objective in Fig. 12 was to investigate the differences between the growth rates of male and female haddock of the same ages, the von Bertalanffy parameters are useful for comparisons between the growth rates of males and females of the ages used but are not always closely related to those of Fig. 11 for which more data points were used. The von Bertalanffy curves and parameters of Fig. 12 are therefore more closely related to those of Fig. 11 for the earlier periods and less in the later periods for which progressively fewer ages were used. With due regard for the difference in growth between sexes and differences due to the smaller number of age-groups included in Fig. 12 than in Fig. 11, the remarks applicable to Fig. 11 regarding period growth and the relation of the von Bertalanffy curves to the data also apply generally to Fig. 12 (see also Fig. 13C and D).

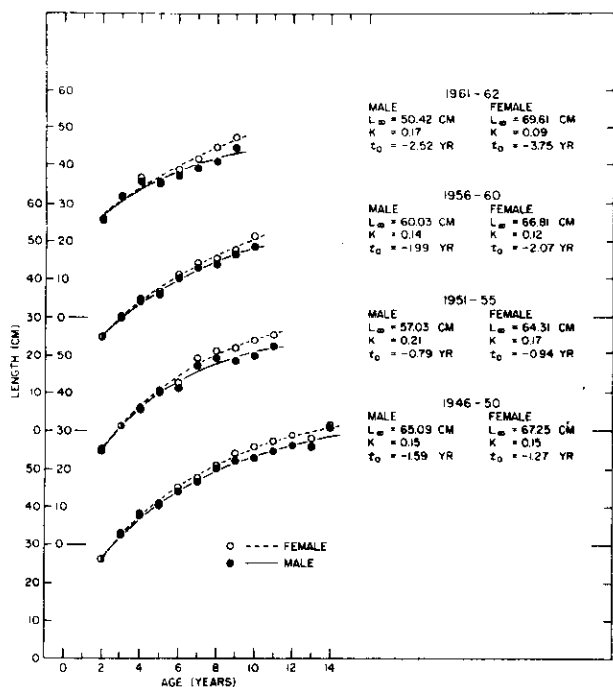


Fig. 12. Average length-at-age (January-June) of male and female haddock from the Grand Bank, in four periods from 1946 and 1962, fitted with von Bertalanffy growth curves. (Mean length-at-age for each sex and age-group based on 3 or more fish per 1,000 and 10 or more fish aged.)

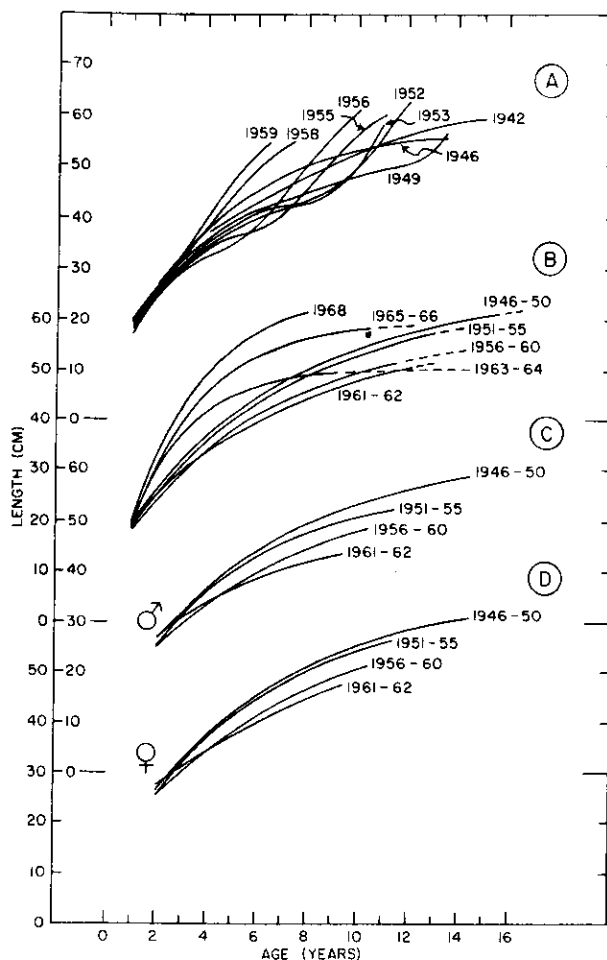


Fig. 13. Comparative relationships of growth curves of (A) year-classes (from Fig. 10); (B) von Bertalanffy curves of period growth (from Fig. 11); (C) and (D) von Bertalanffy curves of period growth for males and females (from Fig. 12). (See Fig. 5 for numbers of fish aged.)

Discussion

Catches and discards

Catches and year-class success. The early peak in catches in 1949 (Fig. 2) was from a previously lightly-fished stock containing many fish aged 10 years and older, in which the 1942 year-class was dominant and in which the 1941 and 1940 and some earlier year-classes were well represented (Fig. 5). The next group of high yields (1955-57) was mainly due to the very successful 1949 year-class, although by 1956 the successful 1952 year-class was contributing to the catch and by 1957 the 1953 year-class also. The final group of high yields in 1960-61 was the product of the very successful 1955 year-class and of the moderately successful 1956 year-class. The ensuing year-classes of 1961, 1962, 1964, and 1966, which were relatively good when compared with the severely reduced year-classes of older fish in 1963-68, were relatively small quantitatively, and the first three

contributed to only small increases in the catches of 1966-67.

Implication of information on discards for management-related studies of the haddock fishery.

The discards at sea were made after the haddock had been selected for commercial use and were all dead. The discard information indicates that the reported nominal catches of haddock, up to at least 1960, were usually considerably smaller than the actual catches. Discards were especially high when haddock of a successful year-class were large enough to be caught but mainly too small to be retained. The greatest discards, and discards of the largest fish, were in the earlier years.

Large numbers of young haddock were discarded, most of which were immature with good potential for growth. However, since the early growth of all successful and moderately successful year-classes of 1949 to 1956 was relatively slow and in view of the relationship between haddock abundance and growth demonstrated in this paper, growth would have been even slower if large numbers of young fish had not been removed from the stock.

It is evident that numbers at age from commercial landings, as in Hodder (1966), can provide only a partial picture of length, age, growth and fishing mortality of the population. In situations where the numbers of fish discarded at sea form a significant portion of the total removals, sampling for length and age should not only be carried out on the commercial landings but also at sea on the actual catches, so that the quantities discarded, or utilized for fish meal, can be taken into account when evaluating the state of the stock and predicting potential yields for management.

Year-class success

Introduction. Sampling of Newfoundland commercial landings and of haddock taken by the USSR during parts of the period under investigation produced approximately similar results as those described in this paper. In landings of haddock from the Grand Bank by Newfoundland commercial trawlers in 1955-64, Hodder (1966) found the 1949 and 1955 year-classes to be most abundant, followed in order of abundance by the 1952, 1953 and 1956 year-classes. For haddock taken by USSR trawlers on the Grand Bank in 6 years between 1954 and 1964, Shestov (1967) reported that the 1949, 1952, 1953, 1955, and 1956 year-classes were most successful. However, they did not usually show as much dominance relative to other year-classes as in our age readings. For haddock samples taken by the USSR from Div. 3N and 3O in 1966-71, Shestov (MS 1972) found that the 1962, 1964 and 1966 year-classes were relatively most abundant, as in our investigations.

Many of the factors influencing or determining year-class success have been discussed in reviews by Hempel (1963, 1965), Cushing (1966, 1969) and Templeman (1965, 1972). The data available for this paper allow the discussion of only a few of these factors.

The most surprising features of the year-class picture as obtained from the survey data are: the great differences in relative numbers, more than 600 to 1, between the most highly successful and the poorest year-classes in the 1940-56 period during which successful year-classes occurred; and the reduction in survival from ages 2-4 to ages 5-7 to an average of 0.05 for the unsuccessful 1958-62 year-classes (survey years 1960-66 for age-groups 2-4 and 1963-69 for age-groups 5-7), compared with 0.50 for the 1952-56 year-classes (survey years 1954-60 for age-groups 2-4 and 1957-63 for age-groups 5-7), a period (1952-56) in which there were two successful and two moderately successful year-classes.

Iceberg number and water temperature. For the Grand Bank haddock, there was a significant inverse relationship between iceberg number and year-class success. The causes of the variations observed in iceberg number are too complex to be considered in detail here, but the main factors may be mentioned. The supply of icebergs in Baffin Bay is very great. Their principal origin is from the West Greenland glaciers from which approximately 15,000 icebergs are calved each year (Dinsmore, 1972). With about 90% of the volume of iceberg under water, currents affect iceberg drift more than winds although winds are important in modifying the direction in which icebergs drift. They last longer and drift farther southwards when the Labrador Current in which they are mainly drifting is cold and flowing strongly, the air is cold, ice cover is great, and winds are northerly or northwesterly. Under these favorable conditions more would drift southward beyond 48°N from a given number drifting from Baffin Bay and Davis Strait than if conditions for any of these factors were unfavorable (Scobie, 1975). For some years, good agreement is recorded between Labrador Current flow and Grand Bank temperatures and iceberg numbers. Soule and Morse (1958) found the largest volume transport of Labrador Current water, occurring in 1957, to coincide with a very severe ice year (931 icebergs south of 48°N). Similarly in the figures presented by Dinsmore and Moynihan (1972), both the volume flow of the Labrador Current and the iceberg numbers were relatively low in 1955 and 1956, 2 years in which successful haddock year-classes occurred. The year 1958 was a warm year on the Grand Bank (Fig. 7) and only one iceberg was noted below 48°N. In 1972 the greatest number of icebergs up to that time (1,587) were recorded south of 48°N. This was a year also of very cold water on the Grand Bank and considerable increase beyond the normal in the flow of the Labrador Current from April to June (Scobie, 1975). However, there is no general relationship, in the figures of

Dinsmore and Moynihan (1972) mentioned above, between high and low volume flow of the Labrador Current and high and low iceberg numbers. These Labrador Current flows, however, were determined from the oceanographic section off southern Labrador in July–August, whereas most of the icebergs, arriving in greatest numbers south of 48°N in March–June, would have passed southern Labrador earlier in the year. However, Dinsmore (1972) said that “The supply of icebergs in Melville Bay and Baffin Bay is virtually inexhaustible. We generally attribute the occurrence of icebergs on the Grand Bank as a function of the volume of the flow of the Labrador Current which has its initial beginnings in Baffin Bay”.

Similarly in our data (Fig. 6 and 7), there is no generally consistent relationship between August average water-column temperatures on the Grand Bank and iceberg numbers and between these temperatures and year-class success. There is, however, a fairly good inverse relationship between iceberg number and temperature in Fig. 7B in 7 of 9 years between 1957 and 1965, but there were no large year-classes in this period and there was no consistent relationship between temperature or iceberg number and relative year-class success. The August temperatures may be too late to be in consistent agreement with either iceberg number or year-class success. Iceberg number is greatest in May (Murray, 1969) and haddock spawning at its peak in June (Templeman *et al.*, 1978). The southern part of the iceberg flow toward the southwestern Grand Bank borders the haddock area (see the iceberg track in Dinsmore, 1972) and the iceberg melting and any unusual Labrador Current conditions which accompany low or high numbers of icebergs would be expected to affect environmental conditions in the haddock area. Adequate data are lacking on the factors which accompany the variations in iceberg numbers. Among these are temperature and wind effects, current flow rates and patterns of drift, and variation in the quantity and variety of plankton food, all of which affect year-class success. It is evident from the occasional exceptions to the inverse relationship between iceberg number and year-class success that other factors are also operating which limit year-class survival in some years with low iceberg numbers.

Relation of a successful year-class to a previous successful year-class. It is possible that a successful year-class may often produce a new successful year-class at or near the age when most of the females of the year-class first mature. If this occurs, it is also likely that the relationship would be especially evident after an intensive fishery develops, leaving few females at and very few above the maturing ages. The successful 1934–36 year-classes occurred 7 years after the successful 1927–29 year-classes, the successful 1940–42 year-classes occurred 6 years after the 1934–36 year-classes, the 1946 year-class 6 years after the 1940 year-class, the 1949

year-class 7 years after the 1942 year-class, the 1952–53 year-classes 6 and 7 years after the 1946 year-class, the 1955–56 year-classes 6 and 7 years after the 1949 year-class. Although the year-classes after 1956 were all poor relative to the successful year-classes noted above (see Fig. 6), some were more dominant than others and the pattern continued (Fig. 5). For example, the 1958–59 year-classes occurred 6 years after the successful 1952–53 year-classes, the 1961–62 year-classes 6 years after the successful 1955–56 year-classes, and the 1964 year-class 6 and 5 years after the 1958–59 year-classes.

In the period studied, there were often two or three successful year-classes, followed by one or more poor year-classes. Thus a maturing year-class may have its greatest reproductive effect on two new year-classes. During the period of intensive fishing activity (1950–60), the second year-class of a successful pair was usually smaller than the first. During the earlier periods of 1927–29, 1934–36 and 1940–42, when fishing intensity was much lower and haddock lived to greater ages, the significant effect on reproduction of a newly maturing group of year-classes lasted longer. It is apparent (Table 3) that fish older than 7 years formed only a small part of age-groups 5 to 7+ after the 1951 year-class, and that after the 1956 year-class there was increasingly rapid reduction in numbers from age-groups 2–7, so that fewer haddock lived to greater ages. Female haddock on the southern Grand Bank were 1, 7, 56, 91, and 97% sexually mature at ages 4–8 in 1947–50. The age at maturity decreased gradually throughout the period of study so that by 1963–66, 1, 48, 94, 98, and 98% of the females were mature at these ages (Templeman *et al.*, 1978).

The explanations of the success of year-classes, at or close to the period when most of the females of a new abundant year-class became mature, may be the increased quantities of eggs available, the quality of the eggs from young fish, the lack of competition by young fish of the earliest ages, and the spawning locality which is presumably shallower for young than for older fish. The last successful year-classes (those of 1955–56) were decimated by the increased fishing in 1960–61, before the females of these year-classes had reached their full potential as spawning fish. There were, however, fairly good quantities of spawning fish available until 1962, but no commercially successful year-classes appeared after 1956 so that some unfavorable factors were present during this period.

Relative numbers at ages 2–4 and 5–7 in relation to fishing intensity and growth rates. The intensity of commercial fishing primarily for haddock was great in 1960–61, was gradually reduced after 1961 and was at a low level by 1964–69. The relative numbers at ages 5–7 to those at ages 2–4 could therefore have been expected to rise instead of falling so greatly after the survey year 1962.

The increased rate of growth of haddock of the 1958-62 year-classes at ages 2-4 in 1961-66, however, made these haddock, and to some degree also those at ages 5-7, relatively more susceptible to capture in the commercial fishery than the same age-groups in the earlier periods. The effect of the increased growth may be noted in the decrease in the age at full recruitment to age 3 for the 1958-59 year-classes and to age 2 for the 1961-62 year-classes (Fig. 8).

Fishing effort for cod in Div. 3N and 3O was considerably lower in 1962-64 than in 1959-61 but by 1967 it had increased to more than twice the 1959-61 level in response to the strong 1964 year-class first caught as age-2 fish in 1966 and in large numbers in 1967 (Pinhorn, 1970). Fishing effort for redfish in Div. 3O increased by more than four times from 1962 to 1965 and continued during 1966-71 at more than twice the level in 1962. The greatest annual catch of redfish in this period was about 20,000 tons corresponding to an effort of about 47,000 hours fishing by trawlers in the 150-400 tonnage class (Parsons and Parsons, 1975). During and after the decline of the haddock fishery, fishing effort for American plaice on the Grand Bank increased from 17,000 hours in 1962 to 100,000 hours in 1969, declining to 74,000 hours in 1972 (Pitt, 1975).

The increased fishing efforts for cod, redfish and American plaice may all have had some effect in maintaining the very low relative abundance of age 5-7 haddock, although the American plaice fishery is conducted in areas where the bottom temperatures are lower than for haddock. The redfish fishery in the shallower parts of the southwestern slope of the Grand Bank would have taken haddock as by-catch and the small-meshed trawls used for redfish would also have taken small haddock. The yellowtail flounder population was increasing on the southern Grand Bank in 1962-68 and catches increased from 1,800 tons in 1965 to 10,500 tons in 1969. This fishery takes place on the shallow-water parts of the Bank where haddock are normally prevalent in summer (Pitt, 1970), but the development of the fishery in the late 1960's could only have affected the later years of age-groups 2-7 of the 1961-62 year-classes.

In the years of unsuccessful year-classes after 1957, the numbers of haddock at the ages when most females mature were relatively much less, compared with younger age-groups, than those occurring in previous periods of successful year-classes (see Table 3), and, especially after 1962, the quantities of spawning females on the Grand Bank were negligible. Consequently, once the population and year-class production were reduced to very low levels, the chances of commercially-successful year-classes appearing were very small. Presumably the very small number of haddock eggs produced in recent years was an important factor limiting year-class success and very likely the principal one.

Total mortality

Total mortality rates for fully recruited age-groups were lowest during the 1948-59 period in which the first two peaks in the catches occurred. Mortality was considerably higher in the early 1960's following the addition of substantial USSR fishing effort of 1960-61 to that of the preceding years. The research vessel sampling in 1960 occurred from 3 April to 12 May, but more than 70% of the nominal catch of haddock on the Grand Bank in that year, including all of the USSR catch (58% of the total catch of all countries), was taken after the sampling period. Consequently, the effect of this increased mortality, if any, would be reflected in the sampling data for 1961. The fishing effort for haddock by USSR was greatly reduced after 1961 and by Canada, the only other nation fishing considerably for haddock at the time, after 1962. Thus, the increased mortality on the 1949, 1952 and 1953 year-classes began at ages 12, 9 and 8 in 1961, on the 1955 and 1956 year-classes at ages 7 and 6 in 1962, and on the relatively small 1958 and 1959 year-classes at age 3 in 1961-62 (Fig. 8). The small 1961 and 1962 year-classes grew up at a time when haddock were relatively scarce, but the total mortality continued to be high ($Z = 1.14$) due to by-catches of haddock taken in fisheries directed towards other species.

The considerably increased mortality of the 1955 and 1956 year-classes, in full effect by ages 7 and 6, compared with the lower mortalities of the older fish of earlier year-classes caught in the same period, was because almost all the USSR effort for haddock in 1960 and much of the effort in 1961 occurred on or near the Southeast Shoal. This shallow-water fishery had a greater effect on the younger than on the older haddock which tend to remain in deeper water (Shestov, 1967). It appears unlikely that the 1955 year-class at age 6 and especially the 1956 year-class at age 5 were fully recruited to the fishery.

The total mortality coefficients derived from the research vessel catch-per-effort data (Fig. 8) were higher than those estimated by Hodder (1966) from catch-per-effort data for haddock landed by commercial trawlers. He indicated that Z was 0.75 for ages 7-10 of the 1949 year-class and 0.9-1.0 for the more recent year-classes (1952, 1953 and 1955). Corresponding values for the research vessel data were 0.95 and 1.06-1.90 over ages 7-12. The mortality values based on samples of the landings of commercial trawlers are probably underestimates. Because of the slow growth of haddock in the mid and late 1950's, some of the smaller haddock at age 7 and possibly at age 8 would have been discarded. Also the introduction of a mesh size regulation (100 mm minimum) in 1957 would have had the effect of reducing the numbers of these age-groups caught relative to their abundance in the population. Both factors would cause a reduction in the slope of the commercial catch curves and result in lower total mortality estimates than those from research vessel

data which are not affected by discarding at sea and codend selection.

It is apparent from the research vessel survey data (Fig. 8) that, even though the codend was lined with small-meshed netting, the research trawl did not take young haddock (ages 1 to 5 or 6) as efficiently as the older age-groups, due possibly to the retention pattern of the trawl and the distribution of immature haddock in the survey area. The apparent ages at full recruitment to the research vessel catches for the 1949, 1952, 1953, 1955 and 1956 year-classes were 7, 4, 5, 7 and 6, which are not very different from those for the same year-classes (7, 7, 6, 6 and 6) in commercial landings from the Grand Bank (Hodder, 1966). It is possible that some of these ages at full recruitment in the commercial fishery would have been lower if the actual catches had been sampled before discarding had occurred. However, the total mortality coefficients derived from the research data were usually greater than those for the same age-groups from the commercial landings and probably reflect more realistically the influence of the commercial fishery on the resource.

The reduction in the age of full recruitment in the research vessel catches for the 1958-59 year-classes to age 3 and for the 1961-62 year-classes to age 2 is apparently due to the effects of the commercial fishery in the area and the increased growth after 1960. Following the decline of the directed haddock fishery in the early 1960's, haddock continued to be taken as by-catch in the increasing fishery for redfish along the southwest slope of the Grand Bank, with smaller codend mesh sizes than the legal minimum used in fishing for haddock, and this presumably contributed to the reduction in ages of full recruitment for these recent year-classes as well as maintaining the relatively high mortality rates ($Z = 1.23$ and 1.14). It is most likely that the rapid decline in abundance of the 1958 and 1959 year-classes, beginning at age 3, was initiated by the intensive haddock fishery on the bank in 1961. Noskov (MS 1962) says that the by-catch of capelin in the USSR haddock fishery in July 1961 on the Southeast Shoal was 5 tons per haul, indicating that large quantities of fish much smaller than age-3 haddock were retained by the trawl. The similar rapid decline in abundance of the small 1961 and 1962 year-classes after age 2, in the absence of a directed fishery for haddock, was also presumably caused by the use of similar trawls for fisheries with regulated mesh size and of small-meshed trawls in fisheries for species unregulated by mesh size.

Growth

During the period of this investigation (1946-68), the growth of haddock on the Grand Bank was reduced as fishing effort increased and increased greatly as fishing effort declined toward the end of the period. The tendency

for the fishery to take the faster-growing fish of a year-class partially recruited to the fishery reduces the size-at-age of the remaining fish of the group under selection, but the reduction in the numbers remaining permits them to grow faster. However, it is difficult to assess the resulting effects of these contrasting growth tendencies.

Growth is, of course, affected by temperature as well as by the availability and quality of food. Water temperatures on the southern Grand Bank were observed to be considerably lower in March 1950 than in March 1951 (Templeman and Hunt, MS 1951), and correspondingly the growth of individual haddock, as indicated by the growth zones of scales and otoliths, was often noted to be much smaller than usual in 1950 and greater than usual in 1951. This can be noted in the decline in size-at-age of fish sampled in the spring of 1951 (Fig. 9) and also by the decline in growth of fish at age 9 for the 1942 year-class and at age 5 for the 1946 year-class, with recovery in the following year when temperature conditions were more favorable (Fig. 10).

There is, however, no indication of temperature change sufficient to cause either the depressed growth rate during the intermediate years of the study period or especially the increased growth rate in the later years. The most likely major cause of the changes in growth was the difference in the abundance of haddock with consequent changes in the amount of food available per fish. Most haddock of the ages under consideration spent the late spring, summer and autumn growing period on the shallow southeastern part of the bank where the temperature pattern was probably that of Fig. 7B, that is, on the average a little higher in the earlier and later years of the study period than in the intervening years. Temperatures in the 1940's were probably relatively high. In the Canadian and American coastal areas of the Northwest Atlantic, temperatures increased in the 1940's to a peak in the early 1950's with a subsequent decline which continued in the 1960's (Templeman (1967) for air temperatures at Torbay, Newfoundland; Lauzier (1967) for sea temperatures at St. Andrews, New Brunswick; Chase (1967) for sea temperatures at Boothbay Harbor, Maine).

In the early part of the study period, when haddock were moderately plentiful even at the greater ages, it is probable that higher temperature conditions allowed moderate growth which was depressed by the exceptionally large 1949 year-class. Under the combined influence of the high density of the successful 1955 and moderately successful 1956 year-classes and the lower temperatures at the time, age-1 haddock were at their shortest length in 1956-58 and age-2 fish in 1959. The effects of the large 1955 year-class and the smaller 1956 year-class were evident up to 1962. Age-1 haddock were scarce after 1957, and consequently age-2 fish were

scarce after 1958, age 3 after 1959, etc. The increase in growth due to less competition for food thus began for age-1 fish in 1959 (growth of 1958), age 2 in 1960, age 3 in 1961 and age 4 in 1961 (growth of 1960). The large catches of 1960 and 1961 greatly reduced the numbers of haddock of the 1955 and 1956 year-classes (the last ones of any significance to appear) and of the remaining fish of the successful 1949, 1952 and 1953 year-classes. This reduction in abundance continued in 1962, which was the last year when haddock of any age were even moderately abundant. Except for the occasional deviation, the length-at-age of haddock of all age-groups from 2 to 11 (or 12) progressively increased from 1962 to 1968 (growth years 1961-67) as haddock became scarcer. The growth rate in the 1960's was much greater for the younger haddock than in the previous high growth period of the 1940's, but it is unlikely that sea temperatures in the area were higher in the 1960's than in the 1940's.

There may have been on the average some increase in temperature on the shallow parts of the bank during the latter period of increasing growth (Fig. 7B) accompanied by a decline in temperature in the overwintering area for haddock along the southwestern slope of the bank (Fig. 7A). However, the general pattern of increased growth occurred from 1960 onwards, as the last commercially successful year-classes (1955-56) grew older and declined in abundance, thus relieving the competition for food by the younger fish of the subsequent less successful year-classes. The greatest reduction in numbers of older haddock and in fish of all ages occurred mainly in 1960-62 and continued in the ensuing years, followed by increased growth of all age-groups but particularly the younger fish. The growth pattern described makes it evident that the progressive reduction in abundance was the basic factor behind the growth increases.

There is evidence that an abundant year-class may affect the growth of an ensuing less abundant year-class. The very successful 1955 year-class appeared to depress the growth of the moderately successful 1956 year-class at least from age-groups 1 to 6, and these two year-classes seem to have depressed the growth of age-groups 1 to 3 of the much less abundant 1957 year-class. The effects of large year-classes in depressing the growth of the same and of subsequent year-classes of haddock have been noted by other scientists. The growth of age-1 haddock in the Skagerrak was considerably higher for the 1937 year-class in February 1938 than for age-1 fish of the 1928 year-class in February 1929. The 1928 year-class at age 1 was 37 times greater than the 1937 year-class at the same age and the entire haddock stock in the area was 24 times greater in 1929 than in 1938 (Andersson, 1938). Raitt (1939), for North Sea haddock at age 2, concluded that the growth rate varied inversely with the population size. An abundant year-class also produced lower-than-expected

growth in a poor year-class of the ensuing year. Sonina (1969) concluded, that, as the Arcto-Norwegian haddock increased in numbers, the growth rate declined first in the members of the most abundant year-class and then in those of the preceding and following year-classes closest to them in body size. When the population density was very great, the growth rate declined in all year-classes; when haddock were not abundant, all year-classes displayed a high growth rate (Sonina, 1965, 1969).

The growth of haddock on the Grand Bank, based on back calculation from scales collected during 1931-35 (Thompson, 1939), was lower for all ages up to age 7 than that for 1968 (Fig. 11, 13B) but agreed reasonably well with that of the 1965-66 growth curve. Thompson considered his age readings from scales to be fairly accurate up to 6 or 7 years of age, and our comparative age readings confirm that scale ages are as accurate as otolith ages up to at least age 6. Haddock were therefore fast-growing in the 1930's. [The growth curves for haddock from Newfoundland and other areas in figure 5 of Thompson (1939) were plotted 10 cm too low.]

The growth differential between males and females is related to the maturation process. Templeman *et al.* (1978) have shown that, although a few males become sexually mature at age 3, and even at age 2 in the most recent period of rapid growth, and some females mature at age 3, most males mature at ages 4-6 and most females at ages 5-7. The decreased growth due to the onset of sexual maturity thus begins about a year earlier on the average in males than in females. Also, as demonstrated by Templeman (1948) for Newfoundland capelin and by Thurow (1970) for Baltic cod, mature male haddock may continue to engage in spawning for a longer period than mature females with consequent greater depletion of reserves of fat and protein. Therefore, the overall effect is that male haddock grow at a slightly lower rate than females after the onset of sexual maturity. However, Homans and Vladykov (1954) found no significant differences between the sexes in the feeding of haddock on the Nova Scotian banks. Similar to our results but starting at earlier ages because of earlier sexual maturity, Thompson (1924) for haddock at the Faroes and Raitt (1933) and Jones (1962) for North Sea haddock reported that the length-at-age for females was consistently greater than that for males.

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Sexual Maturity and Spawning in Haddock, *Melanogrammus aeglefinus*, of the Southern Grand Bank

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Abstract

Investigations of sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, of the southern Grand Bank (ICNAF Divisions 3N and 3O) were carried out from 1946 to 1968. Stages of sexual maturity are described. Mean lengths at 50% maturity declined about 18% for males between 1950 and 1960 and for females between 1952 and 1962, and subsequently increased by 36% for males and 38% for females up to 1966. These changes coincided with similar changes in the growth rate of haddock during the period under consideration. Sexual maturity typically began at age 3 (exceptionally at age 2) in males and at age 4 in females. At age 6 in males and age 7 in females, more than 90% of the fish were mature. As the fishery for haddock increased in intensity and later when haddock became scarce and grew faster, they tended to mature at earlier ages. Mean ages at 50% maturity declined by about 17% for males and 14% for females over the entire period. Faster-growing haddock of an age-group matured at a higher rate than the slower-growing fish. Few haddock spawned before May and after July, with the peak of the spawning in June. Gonad weights of maturing male haddock reached a maximum in March, about 2 months before spawning occurred, whereas the greatest average weight of the female gonad occurred in May when significant spawning began. For both sexes in the ripening condition, larger fish had larger gonads relative to the body weight. One hermaphroditic haddock was found.

Introduction

From an insignificant fishery before 1946, the annual catches of haddock in the Newfoundland area (ICNAF Subarea 3) increased rapidly to a peak of 79,000 metric tons in 1949, declined to 43,000 tons in 1953, rose to a second peak of 104,000 tons in 1955, declined again to a low of 35,000 tons in 1959 and increased to a third peak of 80,000 tons in 1961. After 1961, catches declined rapidly to 14,000 tons in 1963 and gradually to 1,500 tons in 1975, the small quantities in recent years being taken as by-catch in fisheries directed toward other species. Except for 2 years in the mid-1950's when haddock were abundant on St. Pierre Bank (ICNAF Subdivision 3Ps), most of the fish were taken on the Grand Bank (Div. 3N and 3O).

During the period from 1946 to 1968 research vessels

of the St. John's Biological Station conducted trawl surveys on the Grand Bank and collected a large volume of material related to the spawning of haddock and to the size and age of fish in various stages of sexual maturity. This paper describes the results of such investigations spanning the periods of the early development of the fishery, the relatively high exploitation of the stock and its subsequent decline to a very low level of abundance. Some information on spawning and sexual maturity of haddock in this area has been reported by Thompson (1939), Rojo (1959), Shestov (1967) and Serebryakov (1971).

Materials and Methods

Collection and organization of data

The materials and data for this paper were gathered in

1946-68. Although data collected over all months of the year were used in determining the extent of the spawning season, comparisons of length, age, and stage of sexual maturity in haddock were made from data collected during January-June in order to minimize the differences in length-at age due to growth. This restriction also allowed for a more definite distinction between immature and sexually mature or maturing fish that can be made shortly before, during, and shortly after the spawning season. Usually only the data for 1947-66 were used, with occasional reference to the data for 1946 and to the very limited data for 1968.

Data on maturities and gonad stages were collected at sea, mainly by the research vessels *Investigator II* during 1946-64 and *A. T. Cameron* during 1959-68, and occasionally on commercial trawlers. Most of the data were collected during bottom-trawl surveys in Div. 3N and 3O, extending from the northern part of these divisions to the southwestern slope of the Grand Bank at 275 m (Fig. 1). The few samples from commercial trawlers were taken within the same depth range and area. Data were also collected at the Biological Station from haddock samples taken during the last 1 or 2 days of the surveys and stored in

ice. Maturity stages were determined by the authors or, under the supervision of the authors, by technicians and scientists experienced in recognizing these stages in haddock and cod gonads.

The ages of haddock taken during 1946-57 were determined from both scales and otoliths and those for 1958-68 from otoliths with some checking from scales, with 1 January being assigned as the birthdate. Haddock lengths were measured to the nearest centimeter from snout to mid-fork of the caudal fin. Gonad weights were taken in grams and fish weights in pounds to the nearest ounce in the laboratory on balances which were routinely checked and adjusted for accuracy.

For each survey year, the length frequencies of the research catches in January-June were combined, the total length frequency converted to number at length per mille, from which an age, length and sex table was calculated by applying the appropriate age-length key for each sex. After combining these per mille data for analysis by 4-year intervals for age-maturity data, the frequencies were weighted by the number of haddock sampled in the relevant 4-year periods.

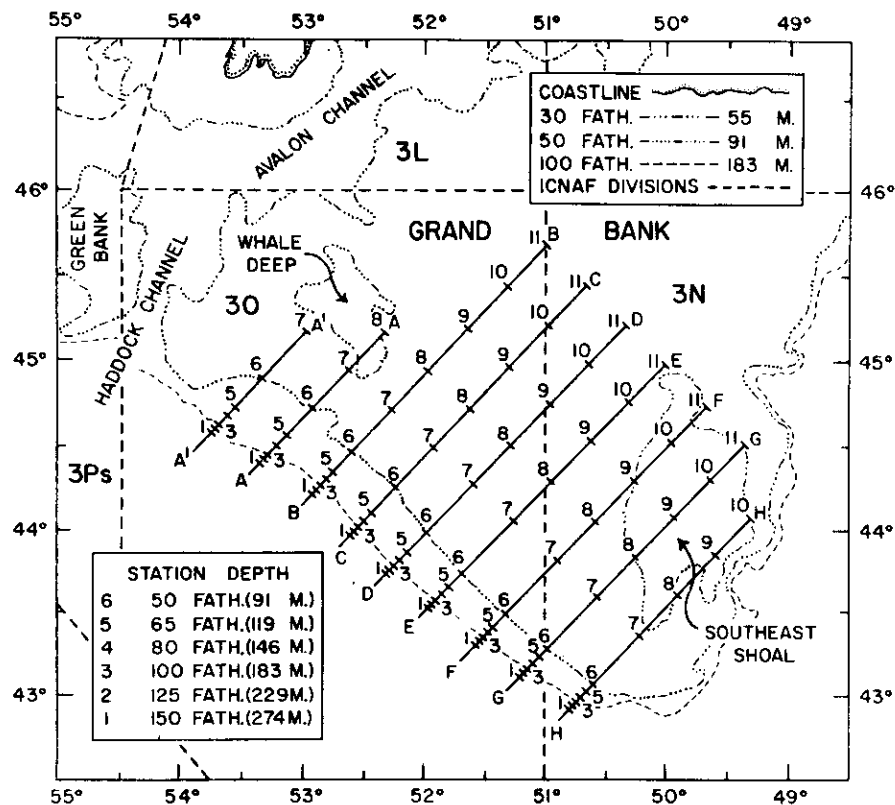


Fig. 1. St. John's Biological Station research-vessel cruise tracks and fishing stations on the Grand Bank (Div. 3N and 3O).

TABLE 1. Description of the maturity stages of haddock used in this investigation.

Male	Female
Imm. Testes narrow and translucent, vasa deferentia very narrow and thin-walled.	Imm. Ovary small, grey to pink in color; membrane thin and translucent; eggs not visible to naked eye.
Spent L. Vasa deferentia wide and opaque, sometimes with residual milt from spawning in previous year; outer edges of testes not pinkish or greyish as in maturing fish; spent in previous (L = last) year.	Spent L. Ovary thick-walled with no new eggs visible to the naked eye; spent in previous (L = last) year.
Mat P. Testes relatively thick compared with immature, with outer edges pink or grey in early stage and white in later stage; early in the year some testes may show evidence of spawning in a previous year but the edges of the testes indicate recovery; maturing to spawn in present (P) year, i.e. year of capture.	Mat A-P. Eggs visible to naked eye in ovary itself; all eggs opaque; maturing to spawn in present (P) year.
Partly Spent P. Some milt extruded in present year, but residual milt in testes and vasa deferentia.	Mat B-P. Opaque and clear eggs present with less than 50% of the volume being clear eggs; maturing to spawn in present (P) year.
Spent P. Spawning completed in present year; recovery not sufficiently advanced for outer edges of testes to be pinkish or greyish in color.	Mat C-P. 50% or more of the volume are clear eggs; this stage also includes the ripe condition where the ovarian content is almost liquid with clear eggs; to spawn or spawning in present (P) year.
Spent P Mat N. Spawning completed in present year; outer edges of testes pink or grey or even becoming white in preparation for spawning in the next (N) year; this stage becomes Mat P in January of the next year.	Partly Spent P. Ovary not full as in Mat C-P; some eggs extruded but many clear eggs remaining.
Mat N. Testes developing from immature stage for spawning in the next (N) year; testes becoming thick, being pink or grey early in this stage and gradually whitening; this stage becomes Mat P in January of the next year.	Spent P. Spawning completed in present year but possibly a few clear eggs remaining; no new opaque eggs visible to the naked eye.
	Spent P Mat N. Spawning completed in present year, and new opaque eggs, for spawning in the next (N) year, visible to the naked eye; this stage becomes Mat A-P in January of the next year.
	Mat A-N. No evidence of previous spawning, but new opaque eggs, for spawning in the next (N) year, visible to the naked eye; this stage becomes Mat A-P in January of the next year.

Maturity stages

The maturity stages used (Table 1) were developed by the senior author in 1946-47. The descriptions apply especially to cod and haddock but are generally applicable to at least the females of other gadoids and the flatfishes. It was found that the usual numerical system for maturity stages did not give the information required to determine precisely the relation of gonad maturity stage, especially in ovaries, to spawning time of individual fish. Because the maturity observations were often made by different scientists and technicians, it was considered preferable to use descriptive stages, including an indication of the year in which the fish will spawn or has spawned, rather than a numerical system, as the former are less subject to error and more readily checked.

Notes on application of maturity stages

Male. From the beginning of the year until the start of spawning in the spring, all males developing for spawning are called Mat P. During this period, the edges of the testes gradually change from grey or pink to white as the testes become full of milt with none or very little in the vasa deferentia. If the testes are white and full of milt, the outer edges rounded, and the vasa deferentia also relatively full of milt, the fish are recorded as Partly Spent. There is no precise way of determining the Spent stage, as there may still be a large amount of milt in the vasa deferentia at the

end of spawning (i.e. when all females are found to be spent) and for some considerable time afterwards. Therefore, when the milt has disappeared from the outer edges of the testes leaving a grey or pink color, it is assumed that spawning is over, even though there may still be milt in the testes and vasa deferentia, and the maturity stage is recorded as Spent P Mat N. In small and young spent males, the testes may lose milt and recover so quickly that it may be difficult at this time to distinguish them from immature males. The Spent P Mat N stage passes gradually to Mat N but may not reach it before the end of the year. Because of the difficulty of making as fine a distinction in the maturity stages for males as for females, spawning dates are best determined from the maturity stages of females.

Female. From the beginning of the year until the start of spawning in the spring, maturing females are recorded as Mat A-P, Mat B-P or Mat C-P according to the prevalence of opaque and translucent eggs in the ovaries (Table 1). During this pre-spawning period, the Spent L stage is assigned only when it is apparent that the fish has spawned in the previous year but has not reached the Mat A-P stage. In the case of spring and early summer spawners, ovaries in the Spent L stage are usually rare, but they may be more frequent in the early part of the year for stocks which spawn in late summer and autumn. After

spawning actually begins, the Spent L stage should not be used as it would be difficult to distinguish between this stage and Spent P. Ovaries recorded as Spent P are whitish-grey or bluish-grey in color, slack and often wrinkled, the membrane being opaque and thick in the older fish even during the early Mat A stage. The contents of the ovary are loose and somewhat mucous, usually with some residual clear eggs and collapsed shells of clear eggs retained from the earlier spawning. The Spent P stage gradually passes to Mat A-N. In younger females, especially those which may have spawned for the first time, the ovarian wall may become thin and translucent during the transition from Spent P to Mat A-N. In such cases, the ovaries may be mistaken for those of immature fish if no residual eggs are present.

In determining the stages of sexual maturity in females, it is not sufficient merely to examine the outside of the ovaries. The ovarian membrane of a fish in the early Mat A-P stage of a spent female may be so thick that eggs are not visible to the naked eye unless the ovaries are cut open. Also, the first clear eggs of the Mat B-P stage are usually near the center of the ovary, and the Mat A-P stage would be assigned unless the ovary is cut and a portion of the egg mass near its center placed in a dish of water for examination. Similarly, an ovary with the appearance of Mat B-P at the surface may often be determined to be Mat C-P when cut, as larger masses of clear eggs tend to occur near the center of the ovary than near the surface. The same procedure should be followed when there is doubt whether the fish is immature or recovering from the spent condition, the latter being detected by the presence of residual eggs or collapsed shells of clear eggs among the ovarian tissue. If the ovary is slack and has lost an appreciable quantity of eggs, it is called Partly Spent.

Analysis of maturity data

The transition from the immature to the mature condition in haddock occurs over a range of length and age in the form of a cumulative normal frequency distribution or sigmoid curve. To facilitate the comparison of trends in length (L_{50}) and age (A_{50}) at which 50% of the fish are sexually mature, a method, referred to as "probit transformation" by Mather (1946) and Fisher and Yates (1953), was used. The method was originally applied by Bliss (1935a, b, 1952) to assess the effects of various doses of poisons and vitamins on animals, and by Stanley and Slatis (1955) in *Tribolium* experiments to determine the time at which 50% of the animals had transformed from one developmental stage to another. The first application of the method, known to the authors, to determine the age at 50% maturity in fish was by Fleming (1960) for cod populations in the Newfoundland area, and Pitt (1966) used the method in his studies on the maturity of American plaice. The "probit transformation" method of fitting a sigmoid curve is described by Fisher and Yates (1953), and a worked example, as applied to age at maturity in cod, is given by

Fleming (1960).

The variances, from which the standard errors (SE) of the L_{50} and A_{50} values were derived, were calculated by the formula for the large sample method given by Fisher and Yates (1953, p. 11). In order to justify the use of that formula, the goodness of fit of the transformed probit values was determined by χ^2 for η degrees of freedom, where $\eta+2$ is the number of length groups or the number of age groups from which the L_{50} and A_{50} values were respectively calculated. In the few cases where the calculated χ^2 exceeded χ^2 for $P=0.05$, the standard errors of the L_{50} and A_{50} values were multiplied by $\sqrt{\chi^2/\eta}$, as suggested by Fisher and Yates (1953, p. 12). The fiducial limits of the L_{50} and A_{50} values were also calculated for Student's $t = 1.96$, but these were so similar to the 95% confidence limits obtained from $L_{50} \pm 2SE$ for the length frequency data (or $A_{50} \pm 2SE$ for the age frequency data) that the latter were used in plotting Fig. 3 and 4.

For testing the significance of the proportions of fish maturing by length group for each age (data of Table 5), based on the hypothesis that larger and smaller fish of an age-group mature at the same rate, the variance test for homogeneity of a binomial distribution was used, as described by Snedecor and Cochran (1967, p. 240).

Combination of January-June data

The sexual maturity determinations, affecting Tables 2-5 and Fig. 2-4, were carried out in the January-June period of 1946-68 and all extended to May or June. In the years 1949, 1950, 1952, 1953 and 1962, observations were taken from January or February to May or June, in 1961 from March to June, and in the remaining years between April and June. It is possible that some young fish, unrecognizable in the early part of the year as spent fish of the previous year and not advanced to the Mat P condition, or immature females with tiny yolky eggs not yet visible to the naked eye, would mature to spawn later in the year. These fish would therefore not be recorded as mature in January-February but would be recognized as such in May-June. This is not likely to have affected the distribution of maturity stages recorded for males, because 90% of the mature and maturing fish were in the Mat N stage by September and all by October-November (Table 6). For females, the relative numbers of immature and mature fish at length and age were compared for January-February, March-April and May-June of 1949, 1950, 1952, 1953 and for February and May of 1962. Differences in the percentages of mature fish in these periods were either negligible or varied in a random way, indicating that there is little error in combining the data for the January-June period. The constant relative weight of the immature ovaries from January-February to May-June (Table 7) and the differences between these and the gradually increasing relative weights of Mat A-P females justify the same conclusion.

Results

Variation in fish length at sexual maturity in different time periods

Figure 2 shows the relative numbers of immature and mature haddock at various sizes for the 1947-66 period, with the data combined by 2-year intervals to provide an adequate base for statistical treatment. The trends in mean length at 50% maturity (L_{50} from probit analysis) are

shown in Table 2 and Fig. 3. For males, the L_{50} values declined from an average of 39.5 cm in 1947-52 to 32.7 cm in 1959-60 and increased to 44.3 cm in 1965-66. A similar trend in L_{50} occurred for females, from an average of 44.4 cm in 1947-52 to a low value of 36.8 cm in 1961-62 followed by a rapid increase to 50.6 cm in 1965-66. The levels of L_{50} in 1965-66 for males and females were significantly higher ($P < 0.001$) than any of the previously high values in 1947-52.

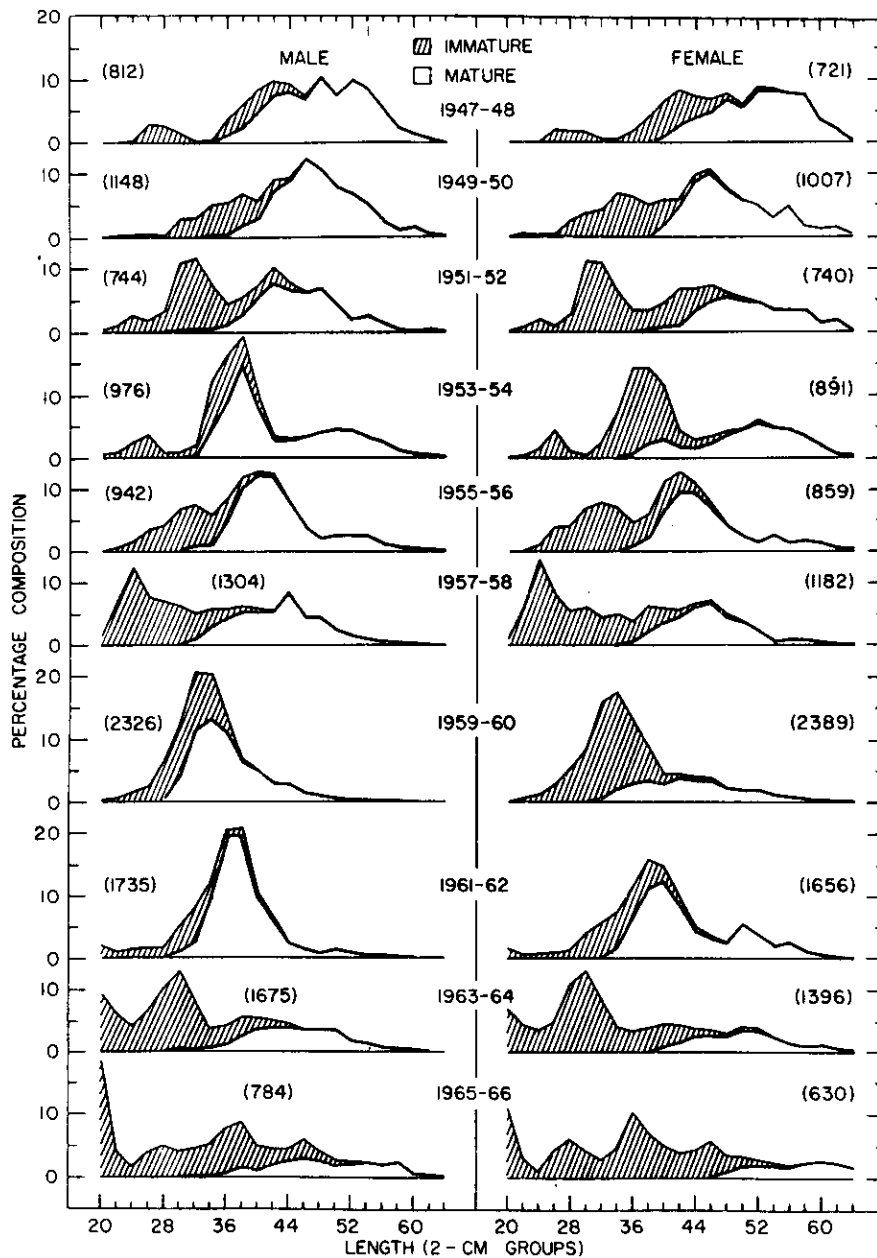


Fig. 2. Percentage frequencies of immature and mature haddock of the Grand Bank by sex and 2-cm length groups (20-21 cm, etc.), January-June 1947-66. (The numbers of haddock examined for sexual maturity are given in parentheses.)

TABLE 2. Mean length (cm) at 50% maturity (L_{50}), range of length between 10 and 90% maturity (L_{10-90}), and standard error (SE) of L_{50} for male and female haddock from the Grand Bank in January-June of 1947-66. (One-half of the L_{10-90} range extends equally on either side of the L_{50} value.)

Years	Male			Female		
	L_{50}	SE(L_{50})	L_{10-90}	L_{50}	SE(L_{50})	L_{10-90}
1947-48	39.45	0.362	10.62	44.29	0.290	9.80
1949-50	39.88	0.195	7.04	43.95	0.316 ¹	6.74
1951-52	39.22	0.281	10.04	44.93	0.320	10.30
1953-54	36.10	0.248	10.40	43.86	0.310	12.06
1955-56	35.88	0.335 ¹	7.54	40.15	0.394 ¹	9.96
1957-58	34.93	0.214	8.00	39.93	0.215	7.00
1959-60	32.66	0.217 ¹	10.34	39.56	0.179	10.52
1961-62	33.39	0.150	7.02	36.77	0.237 ¹	8.84
1963-64	39.09	0.239	10.04	44.02	0.270	9.40
1965-66	44.35	0.619	13.56	50.63	0.596	10.56

¹ χ^2 (as measure of goodness of fit) exceeded χ^2 for $P = 0.05$, and SE (L_{50}) multiplied by the factor $\sqrt{\chi^2/\eta}$ (See Materials and Methods section for explanation.)

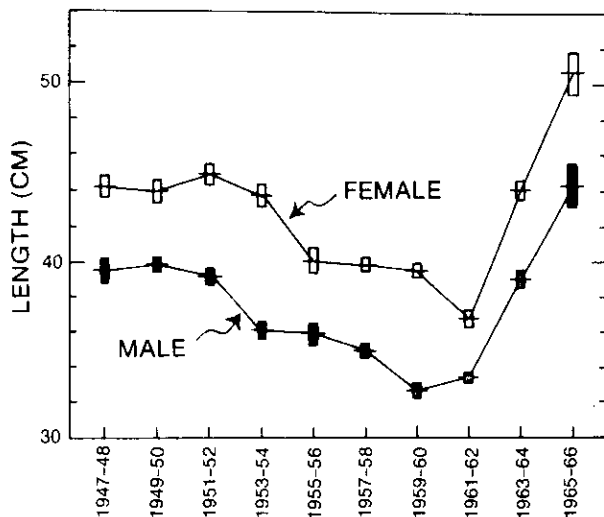


Fig. 3. Trends in mean length at 50% sexual maturity for male and female haddock of the Grand Bank, January-June 1947-66. (The vertical bars represent the 95% confidence limits, i.e. $L_{50} \pm 2$ standard errors. See Fig. 2 for numbers of fish examined.)

The range of length over which sexual maturity occurred was extremely variable from year to year if considered in relation to the frequency distribution of mature fish between 0 and 100% of the maturity ogive. A more realistic measure of the range for comparative purposes is to consider the difference between the lengths at which 10% and 90% of the fish are sexually mature (Table 2). The range (L_{10-90}) for males varied between 7.0 and 13.6 cm and that for females between 6.7 and 12.1 cm. Using the paired-sample t test (Snedecor and Cochran, 1967, p. 94), the differences in range for males and females are not significant ($P > 0.9$).

The rapid declines in the L_{50} values, which occurred between 1951-52 and 1953-54 for males and between 1953-54 and 1955-56 for females (Fig. 3), are attributable to the influx of a large number of the very abundant 1949 year-class (Fig. 2) and a declining growth rate. A similar situation occurred between 1958 and 1962 when the very successful 1955 year-class and the moderately successful 1956 year-class became sexually mature in large numbers and the growth rate declined still further. As indicated by the larger confidence intervals (Fig. 3), the 1965-66 data were less adequate for probit analysis than the data for the preceding periods, due to the scarcity of haddock in the survey catches. Although the L_{50} values for this 2-year period could be determined with a reasonable degree of accuracy, the variances associated with the lengths at 10% and 90% maturity are quite large, and thus the L_{10-90} values for 1965-66 are less reliable.

The rapid increase in L_{50} values after 1961-62 for both sexes resulted from a very rapid increase in growth rate and the lack of successful year-classes after those of 1955 and 1956, as the population became rapidly depleted by large catches in 1960 and 1961. These catches consisted almost entirely of haddock of the 1955 and 1956 year-classes (Hodder, 1966; Hodder *et al.*, MS 1970), both being taken at an age when the females were becoming sexually mature. With no successful or even moderately successful year-classes after that of 1956, the spawning population decreased rapidly after 1962 to a very low level.

Variation in age at sexual maturity in different time periods

No sexually mature male or female haddock were found in about 1,600 age 1 fish examined during the January-June periods of 1947-66. No mature age 2 males

were observed in 1947-62 and only 2% in 1963-66 (Table 3). Only 2-9% (average 5%) of the males were mature at age 3. The transition to the mature condition for males occurred chiefly from ages 4 to 7 during 1947-58, ages 4 to 6 during 1959-62 and ages 4 and 5 in 1963-66. No age 2 or age 3 females were sexually mature (Table 3). In most periods, a few females were mature at age 4 (0-7%, average 2%). The major transition to the mature condition in females occurred from ages 5 to 7 during 1947-62 and from ages 5 and 6 in 1963-66, but the data for the latter period are less reliable due to the small numbers of fish of the older age-groups in the samples. Haddock were essentially mature at age 8, but in certain years occasional individuals were immature up to age 11 for females and to age 12 for males. No immature fish were found among 107 males and 161 females of ages 13-18 years.

The mean age at which 50% of the haddock were sexually mature for each time period was determined by

probit analysis. In view of the almost complete absence of data for certain age-groups in bi-annual grouping, the analysis was carried out on data grouped by 4-year periods (Table 4, Fig. 4). For males, the A_{50} values declined from age 4.9 years in 1947-50 to 4.0 in 1959-62 and 1963-66. For females, the decline was gradual from age 6.0 in 1947-50 to 5.1 in 1963-66. During the first three time periods, the rates of decline in A_{50} were similar for males and females. However, a similar rate of decline continued for females to 1963-66, the decline in A_{50} was unusually rapid for males from 1955-58 to 1959-62 with a slight increase in 1963-66. Over the 1947-66 period, males matured on the average about 1.2 years earlier than females. The pairs of A_{50} values for males and females in each 4-year period are significantly different ($P < 0.001$).

The range between the ages at which 10% and 90% of the fish become sexually mature (A_{10-90}) was chosen as a more reliable statistical parameter than that between 0

TABLE 3. Percentages of sexually mature haddock by age and sex on the Grand Bank in January-June 1947-66. (Numbers of specimens examined in parentheses. The 1947-66 percentages are averages of the percentages for the five 4-year periods.)

Age (yr)	1947-50	1951-54	1955-58	1959-62	1963-66	1947-66
Male						
2	0 (78)	0 (212)	0 (419)	0 (106)	2 (1034)	0.4 (1849)
3	2 (57)	4 (265)	3 (425)	9 (312)	8 (301)	5 (1360)
4	21 (175)	22 (294)	41 (170)	59 (644)	50 (184)	39 (1467)
5	50 (109)	72 (265)	77 (144)	84 (664)	91 (73)	75 (1255)
6	86 (206)	88 (35)	91 (505)	98 (646)	95 (27)	92 (1419)
7	99 (326)	86 (17)	98 (216)	99 (464)	97 (18)	96 (1041)
8	100 (210)	100 (10)	99 (65)	100 (40)	98 (85)	99 (410)
Female						
2	0 (52)	0 (159)	0 (386)	0 (81)	0 (917)	0 (1595)
3	0 (57)	0 (237)	0 (354)	0 (273)	0 (254)	0 (1175)
4	1 (151)	0 (243)	7 (196)	2 (567)	1 (164)	2 (1321)
5	7 (94)	19 (193)	24 (115)	30 (610)	48 (76)	26 (1088)
6	56 (227)	55 (27)	67 (421)	79 (567)	94 (26)	70 (1268)
7	91 (258)	93 (35)	94 (178)	94 (474)	98 (34)	94 (979)
8	97 (229)	100 (9)	99 (59)	94 (50)	98 (75)	98 (422)

TABLE 4. Mean age (years) at 50% maturity (A_{50}), range of age between 10 and 90% maturity [(A_{10-90})] and standard error (SE) of A_{50} for male and female haddock from the Grand Bank in January-June 1947-66. (Data from Table 3. One-half of the A_{10-90} range extends equally on either side of the A_{50} value.)

Years	Male			Female		
	A_{50}	SE(A_{50})	A_{10-90}	A_{50}	SE(A_{50})	A_{10-90}
1947-50	4.89	0.062	2.53	5.95	0.085 ¹	2.23
1951-54	4.58	0.047	2.24	5.78	0.088	2.12
1955-58	4.56	0.120 ¹	2.55	5.58	0.046	2.45
1959-62	3.97	0.090 ¹	2.42	5.46	0.069 ¹	2.09
1963-66	4.04	0.108 ¹	2.41	5.14	0.068	1.53

¹ χ^2 (as measure of goodness of fit) exceeded χ^2 for $P = 0.05$, and SE(A_{50}) multiplied by the factor $\sqrt{\chi^2/n}$. (See Materials and Methods section for explanation.)

and 100% (Table 4), as the latter parameter is difficult to determine accurately and is highly variable. Over the five time periods, the range varied between 2.2 and 2.6 years (average 2.4) for males and between 1.5 and 2.5 years (average 2.1) for females. In all cases the range for males was greater than that for females, but the mean of the differences was not significantly different from zero ($P > 0.05$), using the paired-sample t test.

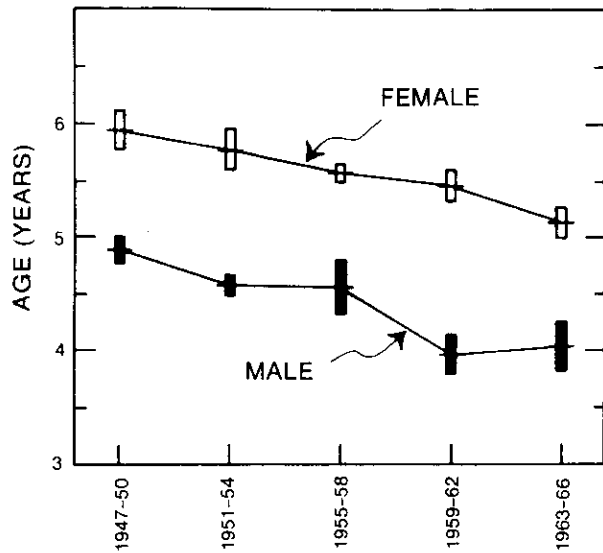


Fig. 4. Trends in mean age at 50% sexual maturity for male and female haddock of the Grand Bank, January-June 1947-66. (The vertical bars represent the 95% confidence limits, i.e. $A_{50} \pm 2$ standard errors. See Table 3 for numbers of fish examined.)

In general, sexual maturity tended to occur at progressively earlier ages throughout the 1947-66 period. Thus, as fishing pressure increased in the late 1940's and was sustained throughout the 1950's up to 1962, a higher percentage of haddock matured at younger ages (Tables 3 and 4, Fig. 4) in spite of a declining growth rate during the period (Templeman *et al.*, 1978). However, during 1963-66 when the population declined to a small fraction of its earlier level and when a great increase in growth occurred, the age at 50% maturity for females continued to decline. The only mature males at age 2 noted during the 1947-66 period were 2% in 1963-64 and 1% in 1965-66. However, from the scanty data available for 1968 (no samples were taken in 1967), 26% of 85 males were found to be mature at age 2, coinciding with a faster growth rate than in any previous period under study (Templeman *et al.*, 1978). Although the numbers of fish in the various age-groups beyond age 2 were small in the 1968 data, there was enough consistency to indicate that the percentages of mature fish at the younger ages were higher than in any of the earlier periods.

Sexual maturity and growth

The varying growth and sexual maturity rates of haddock in the period studied made it advantageous to compare the effect of relative growth in length on age at maturity within year-classes rather than in a combination of year-classes. As can be noted from Table 3, the data for males of ages 4 and 5 and for females of ages 5 and 6 are most useful for comparison, and these data for all year-classes with sufficient data for useful comparisons are included in Table 5. At younger ages few haddock are

TABLE 5. Sexual maturity by length group and sex for various year-classes of haddock from the Grand Bank in January-June 1946-62. (Data sets designated by * and ** indicate significance at probability levels of 0.05 and 0.01 respectively.)

Year-class	Male				Female			
	Age 4		Age 5		Age 5		Age 6	
	Length group (cm)	% mature (numbers of fish)	Length group (cm)	% mature (numbers of fish)	Length group (cm)	% mature (numbers of fish)	Length group (cm)	% mature (numbers of fish)
1942	30-37	0 (32)	34-39	34 (64)**	34-39	0 (40)*	38-45	56 (16)
	38-49	10 (20)	40-49	63 (62)	40-53	15 (62)	46-57	78 (9)
1946	32-37	13 (52)*	34-39	43 (44)**	36-41	8 (59)	34-45	58 (12)
	38-39	25 (51)	40-49	69 (108)	42-49	18 (51)	46-61	62 (25)
	40-45	33 (57)						
1949	30-35	18 (85)*	32-37	88 (88)*	32-39	29 (102)	32-39	48 (44)**
	36-43	31 (100)	38-39	97 (122)	40-49	39 (104)	40-43	64 (158)
			40-57	93 (94)			44-61	87 (126)
1952	30-35	36 (39)	34-37	76 (46)	32-39	23 (62)**	34-41	62 (29)
	36-41	49 (37)	38-39	81 (43)	40-47	63 (49)	42-47	55 (20)
			40-45	92 (25)				
1955	28-31	50 (40)	28-33	65 (89)**	28-33	17 (54)*	32-35	61 (36)*
	32-35	67 (164)	34-35	79 (159)	34-35	30 (148)	36-39	75 (208)
	36-47	70 (76)	36-37	87 (165)	36-37	37 (169)	40-41	79 (102)
			38-49	98 (95)	38-47	39 (157)	42-51	88 (59)
1956	28-31	29 (52)**	28-35	90 (83)	30-35	8 (49)**	32-39	81 (68)**
	32-39	56 (90)	36-47	94 (65)	36-45	33 (64)	40-57	95 (76)

usually mature and at greater ages too large a proportion is mature to provide sufficient contrasts. The different growth and sexual maturity rates of the year-classes and sexes required the use of different length ranges for comparative purposes.

To examine the possible effect of growth in length on age at maturity, the variance test for homogeneity of a binomial distribution (Snedecor and Cochran, 1967) was used, based on the null hypothesis that all fish of an age-group mature at approximately the same rate, irrespective of the size of the fish. For each age-group and sex under consideration (with few exceptions), it is evident that there were smaller percentages of mature fish at the lower length ranges of each data set (Table 5). Many of these differences were significant at the 0.05 and 0.01 probability levels. It is concluded that the faster-growing haddock of an age-group mature at a higher rate than slower-growing fish.

Sexual maturity stages and spawning period

General observations at sea and more detailed examination of specimens in the laboratory indicated that

males had milt in the vasa deferentia for several weeks before there were any females in the Mat C-P stage with eggs ready for spawning. Furthermore, the presence of much milt in the vasa deferentia of most mature males throughout the spawning season indicates that there was always an adequate supply of males to mate with the spawning females.

In view of the difficulty associated with providing a more refined breakdown of the Mat P stage during the ripening of the male gonad, the actual spawning period is best determined from the maturity stages of the female gonad (Table 6). In January-April, some females, designated as Spent L, have not yet recovered to the stage where new eggs are visible to the naked eye. The first evidence of development to the Mat B-P stage was in March and a few females (1%) had even progressed to Mat C-P, but the latter must have been exceptional because no others were found in this stage until the last 10 days of April (0.2%), when a few Spent P females were also observed. Spawning in quantity began in May but less than 10% of the population had spawned up to 10 June. Spawning activity increased during the latter part of June and early July, with

TABLE 6. Percentages of maturing and mature male and female haddock in various stages of sexual maturity from the Grand Bank, 1947-66. (Sp = spent, + = less than 0.5%.)

Month	Number of mature fish	Sp L	Mat A-P ¹	Mat B-P ¹	Mat C-P ¹	Partly Sp P	SP P	Sp P Mat A-N ¹	Mat A-N ¹	Maturing and spawning ²	Recovery after spawning
Male 1947-62											
January	215	1	99	—	—	0	0	0	0	100	0
February	626	0	100	—	—	0	0	0	0	100	0
March	532	0	100	—	—	0	0	0	0	100	0
April	1,016	+	100	—	—	+	0	0	0	100	0
1-20 May	1,287	0	96	—	—	3	1	+	0	100	+
21 May-10 June	864	0	88	—	—	10	2	+	0	98	2
11-30 June	1,085	0	35	—	—	16	25	21	3	51	49
1-20 July	358	0	11	—	—	15	35	33	6	26	74
August	176	0	7	—	—	5	19	46	23	12	88
September	110	0	0	—	—	0	10	85	5	0	100
October	42	0	0	—	—	0	0	2	98	0	100
November	71	0	0	—	—	0	0	17	83	0	100
Female 1947-62											
January	231	2	98	0	0	0	0	0	0	100	0
February	733	14	86	0	0	0	0	0	0	100	0
March	418	4	92	3	1	0	0	0	0	100	0
April	708	3	93	4	+	0	+	0	0	100	+
1-20 May	830	0	57	27	8	1	7	0	0	93	7
21 May-10 June	399	0	33	28	32	1	6	0	0	94	6
11-30 June	760	0	8	16	36	3	37	+	0	63	37
1-20 July	293	0	1	4	9	10	75	1	+	24	76
August	171	0	0	0	1	1	97	0	1	2	98
September	97	0	0	0	0	0	100	0	0	0	100
October	18	0	0	0	0	0	89	0	11	0	100
November	42	0	0	0	0	0	71	17	12	0	100
Female 1963-66											
1-20 May	236	0	60	15	2	0	23	0	0	77	23
21 May-10 June	135	0	45	17	4	1	33	0	0	67	33
11-20 July	68	0	0	6	19	7	68	0	0	32	68
21-31 July	19	0	0	16	5	0	79	0	0	21	79

¹ Mat B-P and Mat C-P not applicable to males, for which Mat A-P = Mat P and Mat A-N = Mat N.

² It is assumed that the Spent L fish will develop for spawning in the year of capture.

about 10% of females in the Partly Spent condition and 76% having completed spawning in the 1-20 July period. Spawning was essentially complete by August. Thus, the main spawning activity of Grand Bank haddock occurred during June and the early part of July.

Post-spawning recovery of adults and the development of immature gonads for first spawning is much slower in females than in males (Table 6), with only 29% of the females in the Spent P Mat A-N and Mat A-N stages in November in contrast to 100% in the corresponding stages for males.

The main part of Table 6, considered above, consists of haddock data for 1947-62. In 1963-66, the percentages of spent females in May and early June were greater than in the same periods of 1947-62. However, the data are somewhat anomalous in that the percentages in the Mat A-P stage were greater than for the corresponding periods in 1947-62 and the percentages of Mat C-P fish were unusually low. In a sample for 11-20 July 1963, the distribution of maturity stages was not greatly different from that for 1-20 July of 1947-62, and a small sample for 21-31 July 1963 indicated that some spawning would have occurred in August.

Variation in gonad weight by maturity stage and season

Relative to the gutted and gilled weight of the fish, the gonad weight of mature male haddock reached a

maximum of 2.4% in March and declined thereafter to 0.8% by the end of the spawning season in August and to 0.5% in September (Table 7). This low value for September, when 85% of the adult males are recovering from spawning (Table 6), may be due in part to the inclusion of a significant number of immature fish whose gonads are developing for first spawning in the following year (Mat N). There was a slight increase in testes weight by November and a more rapid increase to 1.6% by January. The weight of the male gonad is greatest when milt is being developed in the testes. Subsequently, the weight of the testes decreases as milt is transferred to the vasa deferentia, but the gonad weights of Table 6 include the testes, the vasa deferentia and the milt in them. The amount of spawning activity by females in March-April (Table 6) does not appear to be great enough to account for the decrease in the weight of the testes during those months. Therefore the loss in weight of the male gonad before spawning begins may be due to the loss of milt while the fish are being brought to the surface or from pressure of the fish on deck or in ice storage prior to examination in the laboratory.

For mature females, the maximum gonad weight was reached in May (10.2% of fish weight), followed by a decrease to 8.9% in June, and a rapid decrease to 1.7% by the end of the spawning season in August and to 1.5% in September (Table 7). Unlike the situation for males, few females have developed from the immature to the Mat A-N stage by November and very few of those that had spawned previously have developed beyond the Spent P

TABLE 7. Percentage gonad weight relative to gutted and gilled weight for sexual maturity stages of haddock from the Grand Bank, 1947-60. (Numbers of specimens examined in parentheses.)

Maturity stage	Percentage gonad weight of gutted and gilled weight				
	Jan-Feb	Mar-Apr	May-June	July-Aug	Sep-Nov
Male					
Imm	0.1 (29)	<0.1 (18)	0.1 (165)	0.1 (4)	—
Spent L	—	0.3 (1)	—	—	—
Mat P	1.7 (299)	2.1 (356)	1.9 (616)	—	—
Partly Sp P	—	—	2.1 (104)	1.9 (14)	—
Spent P	—	—	1.1 (66)	1.0 (46)	0.8 (12)
Sp P Mat N	—	—	—	0.8 (95)	0.6 (70)
Mat N	—	—	—	0.2 (8)	0.6 (61)
Mature fish	1.6 (166) Jan	2.4 (135) Mar	1.9 (637) May	1.0 (73) July	0.5 (75) Sep
Mature fish	1.8 (133) Feb	2.0 (222) Apr	1.4 (149) June	0.8 (90) Aug	0.7 (68) Nov
Total mature	1.7 (299)	2.1 (357)	1.8 (786)	0.9 (163)	0.6 (143)
Female					
Imm	0.7 (73)	0.7 (107)	0.7 (299)	0.8 (115)	0.8 (127)
Spent L	1.3 (5)	1.2 (11)	1.2 (2)	—	—
Mat A-P	2.6 (334)	4.7 (271)	8.1 (106)	6.1 (1)	—
Mat B-P	—	6.2 (6)	10.7 (179)	8.2 (3)	—
Mat C-P	—	—	12.8 (152)	9.9 (10)	—
Partly Sp P	—	—	4.7 (10)	4.0 (6)	—
Spent P	—	—	1.9 (41)	1.7 (145)	1.6 (147)
Sp P Mat A-N	—	—	—	—	1.9 (7)
Mat A-N	—	—	—	—	1.6 (4)
Mature fish	2.3 (183) Jan	4.6 (125) Mar	10.2 (362) May	3.7 (59) July	1.5 (117) Sep
Mature fish	2.8 (156) Feb	4.6 (163) Apr	8.9 (128) June	1.7 (106) Aug	1.7 (41) Nov
Total mature	2.5 (339)	4.6 (288)	9.9 (490)	2.4 (165)	1.6 (158)

TABLE 8. Percentage gonad weight relative to gutted and gilled weight by size group for maturing male and female haddock from the Grand Bank, 1947-60. (Numbers of specimens in parentheses.)

Months	Maturing males ¹		Maturing females	
	32-47 cm	48-63 cm	32-47 cm	48-71 cm
January-February	1.6 (177)	1.8 (122)	2.3 (117) ²	2.7 (217) ²
March-April	1.9 (223)	2.5 (133)	4.1 (123) ²	5.1 (148) ²
May-June	1.6 (378)	2.2 (238)	7.1 (45) ²	8.9 (63) ²
May-June	—	—	9.1 (57) ³	11.5 (122) ³

¹ Mat P; ² Mat A-P; ³ Mat B-P.

stage. However, by January, the relative gonad weight increased to 2.3%. The ovaries are at their maximum weight when the opaque eggs increase in volume during the transition to the translucent condition. This is clearly evident, especially in May-June (Table 7), from the increasing relative weights observed during the transition from the Mat A-P to Mat B-P and to Mat C-P stages.

For both the males (Mat P) and the females (Mat A-P and Mat B-P) in the ripening condition, the larger fish had larger gonads relative to body weight (Table 8).

Hermaphroditism

A haddock, 46 cm long, caught by the *Investigator II* on 30 June 1957 on St. Pierre Bank and examined by the senior author, was a partial hermaphrodite. The fish was a functional male with white testes (weight 12 g) and milt in the vasa deferentia, some of which may have been lost in the early stage of spawning. Attached to the vasa deferentia near the posterior ends of the testes was a small yellow ovary weighing 2 g, with eggs 0.2 mm in diameter.

Blacker (1971) says that hermaphroditism is absent from published records on haddock sexuality and that consequently, if it occurs as in other gadoids, it must be very rare. We have not noted any other records of hermaphroditism in haddock.

Discussion

Age at sexual maturity

From our investigations, sexual maturity of Grand Bank haddock typically began at age 3 (exceptionally at age 2) for males and at age 4 for females, and more than 90% of the males at age 6 and of the females at age 7 were mature. Males on the average reached maturity more than a year earlier than females. The mean age at 50% maturity in both sexes gradually declined by nearly one year over the 1947-66 period.

Sonina (1969) found that haddock in the southern part of the Barents Sea matured about 2 years earlier in the 1950-65 period than in the 1930's, and attributed this to the

higher growth rate of the 1950-65 period due to the increased abundance of capelin and euphausiids, although water temperatures were lower than in the 1930's.

Thompson (1939), in studies on Grand Bank haddock during 1931-36 (specimens not sexed), found no fish mature at age 2, 16% mature at age 3, 45% at age 4, 95% at age 5 and 100% at age 6. These maturity rates for ages 3-6 are higher than the averages for males and females in any year-group of the 1947-66 period (Table 3). Thompson aged his specimens from scales, compared with our otolith and scale readings, but this should make little difference in age determination up to age 6. Thompson's cruises extended from March to September, but there is no record of when his haddock maturity data were collected. In August and September, many male haddock are maturing for the first time to spawn in the following year (Mat N, Table 6). If these were included in Thompson's data, the age at maturity would have been lower than in our data.

In Rojo's (1959) data for Grand Bank haddock, collected in March-August 1953-55, the percentages mature at ages 3 to 6 were respectively 7, 75, 92 and 97 for males and 3, 73, 85 and 98 for females, with all fish of both sexes being fully mature at age 8. These percentages are higher, especially for females, than in our data for the 1951-54 and 1955-58 periods (Table 3) over parts of which Rojo's data were collected. His percentages for mature females at ages 3-5 were only slightly less than those for males, in contrast to our results which show that females, on the average, mature more than a year later than males. This latter conclusion is, in general, supported by data for haddock from Georges Bank (Clark, 1959) and from the North Sea (Raitt, 1933).

Sexual maturity and growth

From Table 5, it is clearly evident that the faster-growing haddock matured on the average at a faster rate than the slower-growing fish. Similar occurrences have been noted for other areas. Raitt (1933) found that, for each age (2-4 for males and 2-5 for females) at which North Sea haddock were maturing, higher proportions of the faster-growing haddock were mature, and that the differences in the proportions of mature fish of smaller and larger sizes were greater in the younger age-groups. From data on

Georges Bank haddock in March 1949–50 (Clark, 1959), all of the smaller age 3 females were immature, all of the larger females were mature, and the mature fish of this age-group were on the average 7 cm longer than the immatures. Similarly, Sonina (1969) noted that haddock with a high growth rate matured at a earlier age and left the Barents Sea for the spawning grounds off northwestern Norway at a younger age than the slower-growing fish.

Maturing at a younger age is not uncommon in situations where increasing fishing intensity on a stock results in greater growth, as noted in our data after 1962. However, there was also a decrease in the age at sexual maturity during a period of decreasing growth rate due to an abundance of young fish, and this is more unusual and more difficult to explain. Such a reduction in age at maturity could be produced directly by increased fishing on immature fish relative to that on mature fish of the same age groups. It is uncertain whether the immatures and matures of the same age are separate enough on the Grand Bank for this to occur. Also, because the larger fish of a maturing age-group have a higher percentage mature than smaller fish of the same age-group, increased fishing on smaller fish should decrease the average age at maturity. An increased fishery on the smaller fish occurred in the 1950's and early 1960's when larger haddock became scarce and there were often great concentrations of the younger fish of successful year-classes. Additionally, with increasing fishing intensity, fish maturing and spawning at an early age would have relatively more opportunity to produce or to fertilize eggs than those maturing at a later age. If, as is very likely, the early maturing is partly due to a genetic tendency toward early maturity, the age at maturity of ensuing generations should be lowered. Increasing fishing intensity after 1944 could thus tend to produce decreasing ages at maturity by the 1950's from fish derived from spawning of the successful 1942 and 1946 year-classes, and by the late 1950's and early 1960's from those derived from the spawning of the very successful 1949 year-class.

Spawning of individual haddock in relation to maturity stages

On the basis of the information in Table 6, there must be considerable variation in the time when individual haddock develop to the stage where translucent eggs are present in the ovary, and this obviously affects the extent of the spawning season for the population as a whole. The transition of the opaque eggs of the Mat A-P stage to the translucent condition, apparent in the Mat B-P and Mat C-P stages, occurs so rapidly that eggs in an intermediate state of size and semi-transparency are not usually noticed. Sorokin (1957) showed that in stage V cod ovaries containing both opaque and translucent eggs, the latter type were 7 times the volume of opaque eggs. Bigelow and Welsh (1925) found that haddock eggs taken near

Gloucester, USA, in March 1913 averaged 1.57 mm in diameter (1.47–1.72 mm) and were slightly larger than those of cod. Rojo (1959) found the diameter of translucent eggs from formalin-preserved haddock ovaries from the Grand Bank to average 1.47 mm (1.3–1.7 mm).

Taking 1.4 mm as a conservative estimate of translucent egg size and assuming that all of the opaque eggs large enough to be counted in a 54-cm haddock (approximately 1 million, as found by Hodder, 1963) would become translucent, about 1.44 litres of eggs would be produced, or 1.5 kg based on a specific gravity of 1.023 (Bigelow and Welsh, 1925). The average round weight of a 54-cm mature female haddock from the Grand Bank in May–June is 1.5 kg (St. John's Biological Station, unpublished data) and the gutted and gilled weight is 1.2 kg. Thus the weight of translucent eggs that could be produced is equal to the round weight of the fish. Ovaries in the Mat A-P stage (Table 7) averaged 8.1% of the gutted and gilled fish weight in May–June, but this would be somewhat less than the weight of an ovary in which all opaque eggs had reached their greatest size before becoming translucent. Since ovaries in the Mat B-P and Mat C-P stages, containing smaller and larger numbers of translucent eggs relative to the number of opaque eggs, were respectively only 10.7 and 12.8% of the fish weight in May–June, it is obvious that spawning in individual fish occurs over a period of several days as the ovary progresses through the Mat C-P and Partly Spent stages and some spawning may also occur in the latter part of the Mat B-P stage.

Earli (1880), at a fish hatchery in Gloucester, USA, noted that less than 400,000 ripe eggs could be taken in a single day from a 9.5 kg cod containing an estimated 2.7 million eggs, and that the quantity of ripe eggs taken from haddock at any one time was less than that for cod. Meek (1911) noted that spawning by a female cod in an aquarium tank with a mature male, at an average water temperature of 5.5°C, occurred on 6 occasions at intervals of 3 or 4 days over a period of 19 days. Hawkins *et al.* (1967) noted that spawning in captivity occurred on 14 occasions over a 16-day period for a 39-cm haddock of the North Sea.

Sexual maturity and spawning period

On the basis of information for female haddock in 1947–62, a few fish usually began spawning in April, or even in March, but there was very little spawning before the latter part of May. Peak spawning probably occurred in the latter part of June and spawning was mainly completed in July, with occasional spawning in August. Mass spawning in 1963–66 began earlier but extended into July as usual and even to August (Table 6). Testes weights were at their highest in March, three months before most of the spawning occurred in females (Table 7), but this may not be unusual in fish, as Magnússon (1955) found that the

testes of redfish, *Sebastes marinus* (L.), were largest in May–July, although copulation occurred in October–January.

Thompson (1939) reported that 20% of the mature haddock on the Grand Bank were spawning in May. From a small amount of maturity data on haddock collected on the southern part of the Grand Bank in 1953–55 (Rojo, 1959), spawning occurred mainly in June–July. Shestov (1967), for haddock examined in 1954 and 1957–63, concluded that spawning in Div. 3N began at the end of April, attained its maximum in late May and early June and was almost completed in early July, but he had no data from this division for May. For Div. 3O, he concluded that the maximum intensity of spawning occurred in mid-June and that some fish were spawning during the first days of August.

From all of the available evidence, it is concluded that the spawning season for haddock on the Grand Bank extends from April to August, that almost all of the spawning occurs during May–July and that the peak of spawning is usually in June.

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Migrations, Biomass and Stock Interrelationships of Southwest Newfoundland-Southern Gulf Herring from Mark-Recapture Experiments

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Abstract

An extensive tagging program utilizing abdominally inserted tags was conducted in Southwest Newfoundland and the southern Gulf of St. Lawrence during 1970-71 to determine the stock interrelationships and migration patterns of herring populations supporting various seasonal fisheries in these areas. The results of the tagging experiments show that in early April there is an exodus of herring from over-wintering areas along Southwest Newfoundland around Cape Ray westwards across Cabot Strait onto the Magdalen Shelf area. These herring, consisting of a mixture of spring and autumn spawners subsequently move farther westwards into the southern Gulf of St. Lawrence for spawning and summer feeding. Emigration from the southern Gulf occurs in October-November and biological data indicate that these are southern Gulf herring en route to over-wintering areas along Southwest Newfoundland. The significant implication of these findings is that the mobile fleet fisheries which developed along Southwest Newfoundland and in the southern Gulf in the late 1960's were based not on different stocks but rather on one southern Gulf stock complex which was fished at different times and places along its seasonal migration route. The southern Gulf stock complex was therefore being exploited almost year-round and this fact alone increased the probability that fishery removals contributed significantly to the sharp decline in herring landings in recent years.

Introduction

It was the sequential timing of the mobile fleet herring fisheries in the Southwest Newfoundland-Gulf of St. Lawrence area which led Hodder (1966, 1969) to suggest that these herring, like the cod of the same area (Templeman, 1962), probably exhibit a seasonal migration between the Gulf of St. Lawrence and the south coast of Newfoundland. Just prior to the start of the winter fishery along Southwest Newfoundland (hereinafter also referred to as Area J, Fig. 1) a brief but intensive fishery usually occurs at the Magdalen Islands (Fig. 1) in late October and November. A similar fishery takes place there in April-May following the termination of the fishery along the southwest coast of Newfoundland. From July to September the mobile fleet prosecutes a summer fishery in the southern Gulf of St. Lawrence, (hereinafter also referred to as Area T, Fig. 1) particularly the Chaleur Bay-Gaspé area (Fig. 1). These

observations combined with detailed information on the temporal and spatial distribution of herring catches within the Southwest Newfoundland coastal area (Hodder, 1971) indicated that the herring fisheries which developed in Areas T and J in the mid-1960's were not based so much on different stocks but rather mainly on parts of the same stock complex at different times and places along the seasonal migration route. To test this hypothesis the St. John's and St. Andrews Biological Stations of the Fisheries and Marine Service of Canada initiated an extensive tagging program along southwestern Newfoundland and in the southern Gulf of St. Lawrence in 1970 and 1971. This report documents the results of those tagging experiments.

Methods and Materials

Type of tag and tagging equipment

The nature of the herring fisheries in Areas T and J at

the time tagging experiments were contemplated (bulk catches up to 400 tons by purse-seining), the method of unloading (suction pump) and the method of processing (industrial production into meal and oil) necessitated the use of a tag which would remain with the tagged fish during transportation and unloading operations and which could also withstand the rigors of the fish-meal operation (cooking, drying, pressing and grinding). A perusal of the literature suggested that an internal magnetic tag might be the most appropriate tag to use. The feasibility of tagging herring internally with magnetic tags was first demonstrated by Rounsefell and Dalgren (1933) and the method has since been successfully used to delineate the migration patterns of herring on the Pacific coast of Canada (Hart and Tester, 1937; Tester, 1944), and in the Northeast Atlantic (Fredricksson and Aasen, 1950, 1952; Aasen *et al.*, 1961; Dragesund and Haraldsvik, 1968). It was therefore decided to use the internal magnetic tagging technique as the main method of marking.

The tags, obtained from Bergen-Nautik, Norway, were made of #430 stainless steel and were 19 mm long, 4 mm wide and 1 mm thick with rounded ends (Fig. 2). These were coded in lots of 100 tags with each tag in a lot having the same code number. Insertion of the tag, normally between the skeletal element of the pelvic fins, was accomplished by use of a pointed scalpel (Fig. 2).

Method of capture

Area J. Over-wintering schools of herring along Southwest Newfoundland are usually concentrated in small coves within protected bays (Hodder, 1970). This type of distribution is ideal for bar-seining which is not only capable of catching large quantities of herring but can also contain them for several days without significant mortality. Consequently, two bar-seines were obtained, a large one 160 m long and 16 m deep which was used to bar herring

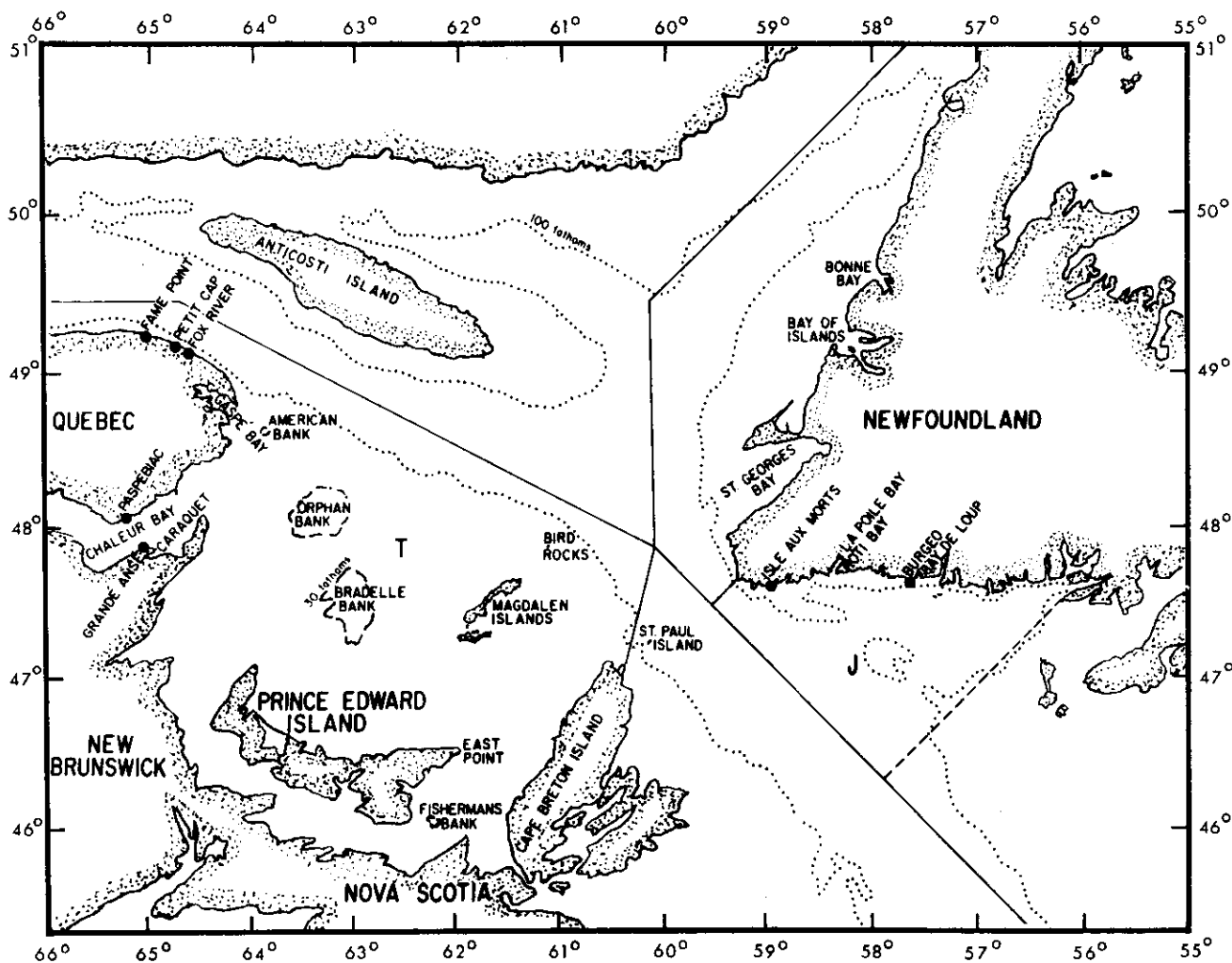


Fig. 1. Area map showing place names mentioned in text.

within a small cove, and a "dipper" seine 135 m long and 16 m deep which was used inside the main seine when small quantities of live herring were required for the tagging operations. A 28-ft motorboat equipped with a portable Simrad echo-sounder was used in the search and detection of herring in the shallow coves and bays.

Two small-meshed holding pounds, one rectangular and one tri-angular, both 5 m deep by 6 m on each side and having an impoundment capacity of 10,000 herring, were used for holding herring during the tagging activities. These were buoyed up by 10-inch diameter floats and were normally attached on one side to the headrope of the main bar-seine.

Area T. In the Magdaiens (Fig. 1) experiment fish were obtained from commercial herring traps and held in holding pounds or free-flooding barges. The holding pounds were 1.2 m on each side and 3.5 m deep with a rigid frame on the top (wood) and bottom (steel) only, the sides being made of 1-inch mesh netting. The free-flooding barges were of the type used by commercial fishermen and were capable of

holding 10,000 fish compared with about 700 in the holding pounds; additionally the barge provided a stable tagging platform and allowed fish to be transported away from the commercial traps to sheltered bays where tagging could proceed independent of sea conditions.

In the Gaspé (Fig. 1) experiment herring were obtained from commercial purse-seines at the "drying-up" stage and were transferred directly into a specially constructed, self-propelled barge (Beckett, in preparation) based on the principle of the larger barges used in the Magdaiens.

Tagging procedure

The tagging operation took place either in free-flooding barges or in two small boats secured to the side of the holding pound and equipped with plastic or canvas tagging tanks capable of holding 50-75 herring each. Live herring were dipped from the holding pound (Fig. 3A) into the tagging tanks using a small-mesh (5 mm) dip-net specially designed to minimize handling injury and scale loss. A tagging team consisted of two individuals seated opposite each other with the tagging tank between them. Herring were removed individually from the tagging tank

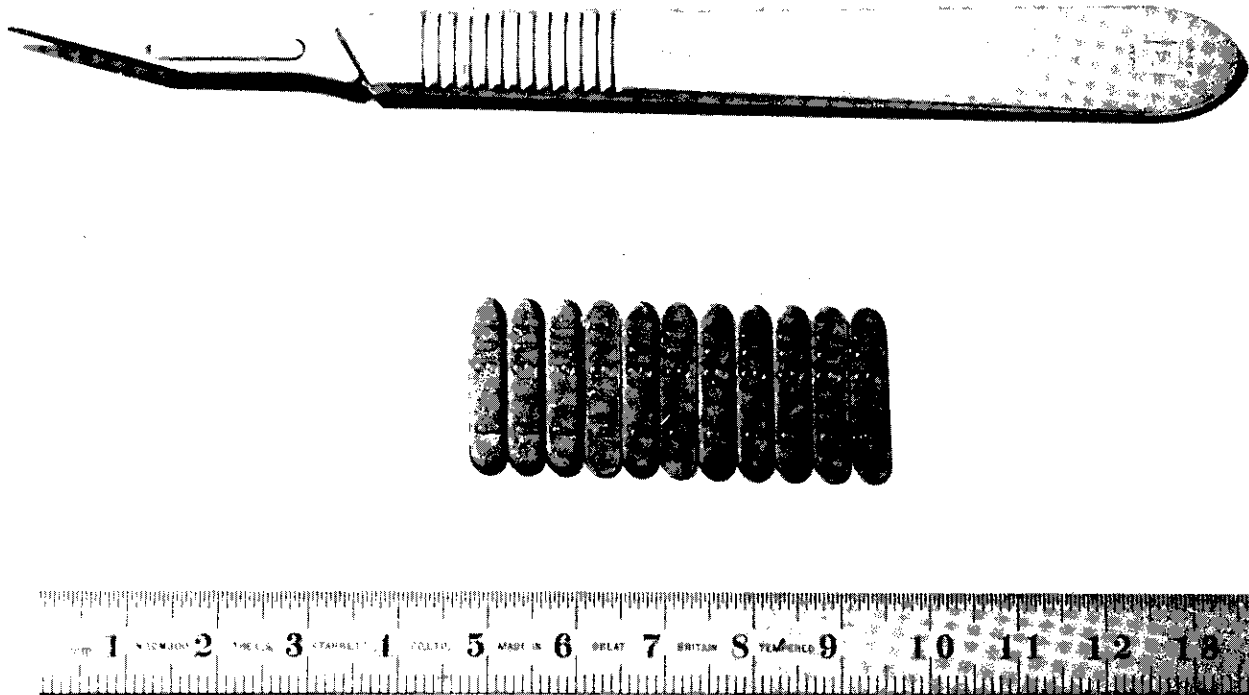


Fig. 2. Tags and tagging utensils employed in the Southwest Newfoundland — southern Gulf tagging experiments.

and held belly-up by one member of the tagging team (Fig. 3B) while the other member made a small incision in the belly of the herring just anterior to and slightly dorsad the pelvic fins using a pointed scalpel (Fig. 3C, D). The metal tag, sterilized in ethyl alcohol was then pushed forward into the abdominal cavity (Fig. 3E, F). Before being released the tagged herring was flexed several times to ensure that the tag was completely inside the body cavity. Small herring (<280 mm) or herring exhibiting considerable scale loss were rejected as unsuitable for tagging purposes and observations were made on environmental conditions, predators and dead tagged fish. Under good conditions a tagging team could mark and release 350-400 fish per hour. Samples of herring from the same batch as those used in the tagging experiments were collected for detailed

biological analyses.

Tagging operations

Area J. Two tagging experiments were carried out along Southwest Newfoundland, one in 1970 and the other in 1971. The 1970 taggings were scheduled to take place in the spring just prior to the disappearance of the overwintering schools of herring from Southwest Newfoundland whereas the 1971 releases were designed to provide additional information on the local movements of herring along Southwest Newfoundland.

During the periods 3-5 March 1970, and 7-8 March 1970, there were two liberations of 8,400 and 4,800 tagged



Fig. 3. Method of internal tag insertion. See text for explanation.

Table 1. Tagging and release information for the various tagging experiments carried out along Southwest Newfoundland and in the southern Gulf of St. Lawrence.

Liberation series	Date tagged	Method of capture	Area of release	Number released
A1	3 March 1970	Bar seine	Lapoile Bay, Nfld.	1,100
	4 March 1970	Bar seine	Lapoile Bay, Nfld.	4,600
	5 March 1970	Bar seine	Lapoile Bay, Nfld.	2,700
A2	7 March 1970	Bar seine	Lapoile Bay, Nfld.	4,500
	8 March 1970	Bar seine	Lapoile Bay, Nfld.	300
A3	11 March 1970	Bar seine	Roti Bay, Nfld.	2,000
	12 March 1970	Bar seine	Roti Bay, Nfld.	7,000
	13 March 1970	Bar seine	Roti Bay, Nfld.	2,800
TOTAL A				25,000
B1	5 May 1970	Herring trap	Gros Cap	2,100
B2	6 May 1970	Herring trap	Gros Cap	3,500
B3	9 May 1970	Herring trap	Anse a Painchaud	15,100
B4	10 May 1970	Herring trap	Anse a Painchaud	8,624
B5	11 May 1970	Herring trap	Anse a Painchaud	6,318
TOTAL B				35,642
C1	14 August 1970	Purse seine	Paspebiac, Que.	1,999
C2	15 August 1970	Purse seine	Fox River, Que.	2,035
C3	15 August 1970	Purse seine	Fox River, Que.	2,699
C4	15 August 1970	Purse seine	Peht Cap, Que.	2,800
C5	16 August 1970	Purse seine	Fame Point, Que.	2,069
C6	16 August 1970	Purse seine	Grande Anse, Que.	2,897
C7	16 August 1970	Purse seine	Grande Anse, Que.	3,594
C8	17 August 1970	Purse seine	Fame Point, Que.	2,374
TOTAL C				20,467
D1	25 January 1971	Bar seine	Bay de Loup, Nfld.	4,200
	26 January 1971	Bar seine	Bay de Loup, Nfld.	5,800
TOTAL D				10,000

herring respectively in LaPoile Bay (Fig. 1) and during 11-13 March 1970, a further 11,800 herring were tagged and released in Roti Bay resulting in a total release of 25,000 tagged herring (Table 1). Samples of herring selected randomly from fish used for tagging purposes were found to be similar in length and maturity composition to those sampled from the commercial fishery during March (Fig. 4). Water temperatures in the tagging localities ranged from 1° to 3°C in the upper 150 m and air temperatures ranged from -5° to 5°C during the period of tagging.

The 1971 tagging experiment was conducted earlier in the fishing season (25-26 January) and farther east (Bay de Loup (Fig. 1)) than the 1970 liberations and fewer tags (10,000, Table 1) were applied. Length and maturity data (Fig. 4) reveal that the herring used for tagging were comparable in such parameters to the commercial catches that were landed in January. Water temperatures ranged from -0.5° to 3°C in the upper 150 m and air temperatures varied within the same range. A severe windstorm occurred on the night of 25 January 1971, and it was noted on the following day that the fish held over-night in the holding pound were lethargic and exhibited substantial scale loss.

Area T. In the Magdalens experiment a total of 35,642 herring were tagged and released from 5 to 11 May 1970 (Table 1) with the bulk of the release being made in

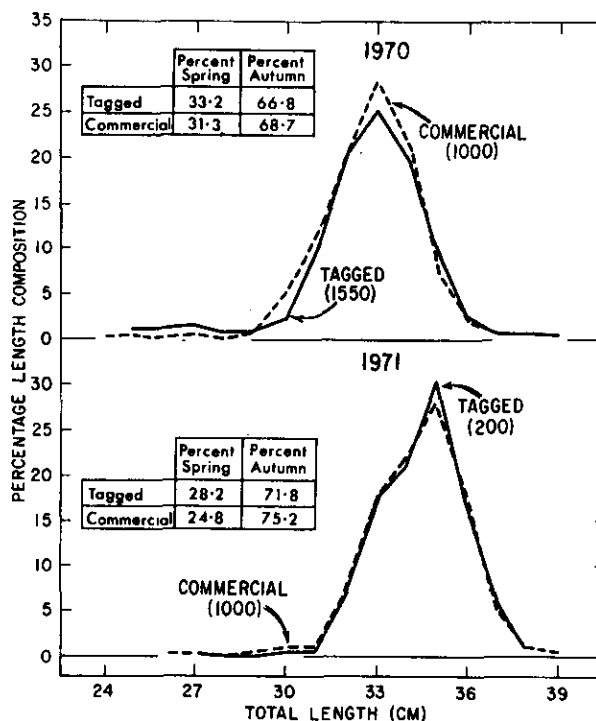


Fig. 4. Length and maturity composition of herring samples in the commercial fishery along Southwest Newfoundland in 1970 and 1971, and those involved in the 1970 and 1971 tagging experiments.

Pleasant Bay (Fig. 1). These herring ranged in length from 26 to 37 cm and were predominantly fecund, frequently spawning in the barge or holding pound. The distended gonads of the ripe fish slowed the tagging rate since it was difficult to make a belly incision without rupturing the gonads.

In the Gaspé experiment a total of 20,467 herring were tagged and released during 14-17 August 1970 with the bulk of the releases being made between Fox River (Fig. 1) and Grande Valtee on the Gaspé coast. Length measurements of fish used for tagging ranged from 26 to 36 cm with a wide range of maturity stages between immature and recovering spent but with no ripe or running fish.

Tag recovery

The internal tags were to be recovered by magnetic separators normally installed (after the drying operation) in the processing lines of reduction plants. An extensive advertising campaign covering all plants receiving herring from the areas under consideration was conducted just prior to the tagging experiments through use of wall posters and contacts with plant employees. At each plant specific personnel (usually the shift foremen) were designated to check magnets regularly and to return any recovered tags along with the pertinent recapture information to the St. John's Biological Station. An incentive reward of \$1.00 was paid for each tag returned.

Method of population size estimation

The estimation of population size from recaptures of tagged fish is based on the assumption that the tagged and untagged fish are caught in the same proportion. In the single census or "Petersen" type (Ricker, 1958) tagging experiment this may be expressed mathematically in the following way:

$$\frac{R}{M} = \frac{C}{N}$$

where R = number of recaptured tags

M = number of fish tagged

C = catch or sample taken for census

N = population size at time of marking.

Bailey (1951) and Chapman (1951) have shown that the above relationship tends to over-estimate the true population size with ordinary direct sampling and they propose modified formulae which give an almost unbiased estimate, of which Bailey's is as follows:

$$\frac{R+1}{M} = \frac{C+1}{N}$$

from which the population size can be estimated as follows:

$$\hat{N} = \frac{M(C+1)}{R+1}$$

An unbiased maximum likelihood estimate of the rate of exploitation according to Leslie (1952) is given by

$$\hat{\mu} = \frac{R}{M}$$

Confidence limits for $\hat{\mu}$ can be obtained in the usual statistical manner. Confidence limits for estimates of population size can be obtained by multiplying the limits of $\hat{\mu}$ by R and then substituting these limits in the above population size equations. Confidence limits for N can also be derived by treating R as a binomial or Poisson variable, obtaining limits for it directly from Clopper and Pearson's (1934) chart and substituting these in the population size equation (Ricker, 1958).

Results

Tag recaptures

The occasional mixing of herring from widely different areas of capture in the storage tanks at reduction plants, together with the time delay between the initial processing phase and the recovery of the tags in the dry meal line meant that it was not always possible to assign a specific area of capture for each recovered tag, except in those cases when the entire fleet was fishing in the same general locality or when individual landings were widely separated in time. Consequently assignment of areas of capture could not be made for some tag recoveries and these are listed as doubtful in Tables 2, 3, 4 and 5.

Within a week after the first liberation of tagged fish of the 1970 experiment, tag recoveries were being reported from the reduction plant at Isle aux Morts and by the end of the winter fishery along Southwest Newfoundland in mid-April 1970, a total of 391 tags were recovered from landings of herring caught in that area (Table 2).

Following the disappearance of herring from Southwest Newfoundland in mid-April 1970, the mobile fleet shifted their activities to the St. Paul Island-Magdalen Island area (Fig. 5A) and 51 tags were recovered during the last half of April from landings of herring caught in that area. During early May fishing was mainly centered around the Bird Rocks area (Fig. 5A) and 13 were recovered from catches in that area.

TABLE 2. Summary of returns from herring tagged in Southwest Newfoundland in March 1970. Plus signs indicate probable areas of capture of tags recovered from mixed landings.

Year	Month	Newfoundland south coast	St. George's Bay	St. Pauls-Bird Rocks	Orphan Bank-Bradelle Bank	American Bank-Gaspé Coast	Fishermen's Bank	Doubtful	Total returns	
1970	March	282							282	
	April	109	—	51					160	
	May	—	—	13					13	
	June					4			4	
	July					23			23	
	Aug					24	2	1	27	
	Sep				+	24	—	2	26	
	Oct				2	+	2	22	26	
	Dec	7							7	
	1971	Jan	44							44
		Feb	41							41
		March	24							24
April		8	2	+				2	12	
May				3					3	
June						3			3	
July					2	5			5	
Aug					+	5		6	11	
Sep						7			7	
Dec		5							5	
1972		Jan	8							8
		Feb	4							4
	March	1							1	
	April		2						2	
	July				+	8		3	11	
	Aug					4			4	
	Dec	1				1			2	
	1973	April		3						3
May				2					2	
Total		534	7	69	4+	108	4	36	762	

TABLE 3. Summary of returns from herring tagged in Southwest Newfoundland, January 1971. Plus signs indicate probable areas of capture of tags recovered from mixed landings.

Year	Month	Newfoundland south coast	St. George's Bay	St. Pauls-Bird Rocks	Orphan Bank-Bradelle Bank	American Bank-Gaspé Coast	Fishermen's Bank	Doubtful	Total returns	
1971	Jan	2							2	
	Feb	275							275	
	March	103							103	
	April	24	3	+				3	30	
	May			4					4	
	July					6			6	
	Aug					4			4	
	Sep				+	+		2	2	
	Oct					3			3	
	Dec	2							2	
	1972	Jan	6							6
		Feb	10							10
April			2						2	
July						7			7	
Aug						1			1	
Sep					+	2		3	5	
Oct						2			2	
1973		April		1						2
	July					1			1	
Total		422	7	4+	+	26+		8	467	

TABLE 4. Updated tag returns from tagging experiments conducted by the St. Andrews Biological Station at the Magdalen Islands, May 1970 (Beckett, MS 1971).

Year	Month	Newfoundland south coast	St. George's Bay	St. Pauls-Bird Rocks	Orphan Bank-Bradelle Bank	American Bank-Gaspé Coast	Fishermen's Bank	Doubtful	Total returns
1970	May			45					45
	June								
	July					1		1	2
	Aug				3			5	8
	Sep				1	4			5
	Oct				1		1		2
	Dec	2							2
1971	Jan	9							9
	Feb	10							10
	March	7							7
	April	5		13					18
	May			1					1
	July					1			1
	Aug				2	4			6
	Sep					5	1		6
1972	Feb	4							4
	July					3			3
	Aug					1			1
	Sep					2			2
	Oct					2			2
1973	April		2						2
	Unknown								5
Total		37	2	59	7	23	2	6	141

TABLE 5. Updated tag returns from tagging experiments conducted by the St. Andrews Biological Station in Chaleur Bay-Gaspe area, August 1970.

Year	Month	Newfoundland south coast	St. George's Bay	St. Pauls-Bird Rocks	Orphan Bank-Bradelle Bank	American Bank-Gaspé Coast	Fishermen's Bank	Doubtful	Total returns
1970	Aug				61+	17+	1	6	85
	Sep				7+	59+	8	19	93
	Oct				13+	58+	10+	7	106
	Nov			1					1
	Dec	30							30
1971	Jan	115							115
	Feb	86							86
	March	77							77
	April	25+		20+				3	48
	May			9					9
	June					2			2
	July				9+	81+		11	101
	Aug					65	14		79
	Sep					42			42
	Dec	6							6
1972	Jan	10							10
	Feb	18							18
	June					2			2
	July					100			100
	Aug					39			39
	Sep					37			37
	Oct					6			6
1973	April		2						2
	Aug					4			4
	Unknown								6
Total		367+	2	30+	108+	512	33	46	1,104

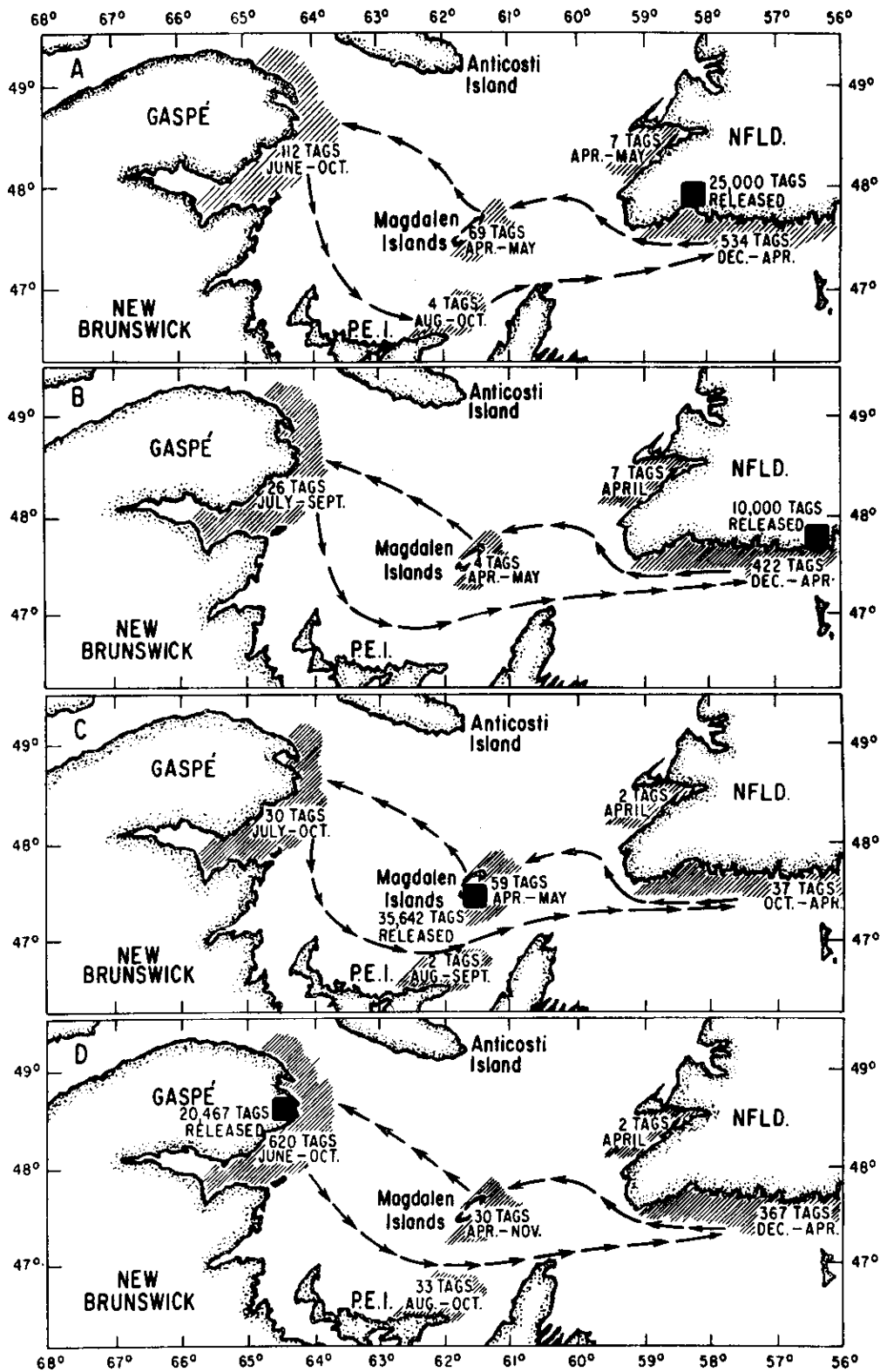


Fig. 5. Tag release and recovery areas for the 1970 Area J tagging experiment (A), the 1971 Area J experiment (B), the 1970 Magdalen's releases (C) and the 1970 Gaspe releases (D).

Gulf herring generally disperse in mid-May, during spawning (spring-spawners) or feeding (autumn-spawners) and fishing operations become less frequent. Intensive fishing did not resume until late June at which time several tags were recovered from landings of seiners fishing on American Bank (Fig. 5A). From July to mid-August fishing was restricted to the American Bank-Gaspé Coast area from Fox River (Fig. 5A) to Chaleur Bay and a total of 38 tags were recovered during this period mainly from the reduction plants in Chaleur Bay. Two tags were also recovered at the reduction plant at Souris, Prince Edward Island, from landings of seiners fishing in the East Point-Fishermen's Bank area (Fig. 5A) in late August. Fishing operations spread to Orphan and Bradelle Banks (Fig. 5A) in September-October and tag recoveries were reported from these areas as well (Table 2). Total tag returns from the spring and summer fisheries in the southern Gulf of St. Lawrence in 1970 were 170.

The usual autumn fishery near the Bird Rocks failed to materialize in November 1970, due to scarcity of fish and the Area J fishery was several weeks late in starting. Consequently the next tag returns were reported in early December from seiners fishing near Burgeo, Newfoundland. From December 1970 to April 1971, a total of 124 tags from the 1970 Area J tagging experiment was recovered from landings of herring taken in Area J.

In the spring of 1971 herring spawning grounds in Pleasant Bay, Magdalen Islands were declared off-limits to all mobile gear with the result that some purse-seiner effort was diverted to the St. George's Bay area (Fig. 5A) where at least two tags were recovered from a total landing of 3,700 tons in late April 1971 (Table 2). In addition at least three tags were recovered from catches made mainly in the Bird Rocks area in late April-early May.

A total of 28 tags from the 1970 releases were recovered during the summer fishery in Area T in 1971 (Table 2). The areas of recapture of these tags were basically the same as in 1970 with the bulk of the returns coming from the American Bank-Gaspé Coast area. Due to scarcity of fish the autumn fishery near Bird Rocks again failed to take place in 1971.

The next tag recoveries were from landings of catches made along Southwest Newfoundland during the 1971-72 winter fishery and in this second winter after tagging only 18 tags were recovered. However, during that season herring landings in Area J suffered a substantial decline from the 1970-71 season (107,000 to 37,500 tons) and in addition a substantial proportion (40%) of the 1971-72 landings were processed as human food, a handling method which does not detect the type of tag used. Two tags were recovered from a small fishery in St. George's Bay during April 1972, and 16 tags were recovered during the 1972 summer fishery in Area T, again mainly from catches made in the American Bank-Gaspé area.

Only one tag was retrieved from the regular winter fishery along Southwest Newfoundland during 1972-73, but only low recoveries were anticipated because of the combination of low landings (<4500 tons) and high utilization for food. Only three tags were recovered from the 1973 spring fishery in St. George's Bay where over 14,000 tons were caught but only about 5,000 tons were processed as industrial fish.

Total returns from the 1970 Southwest Newfoundland tagging experiment to May 1973, were 762 tags, a recovery percentage of 3.03%.

Tag recaptures from the 1971 tagging experiment (Table 3) followed much the same pattern as those from the 1970 liberations. Initial recoveries from this experiment were reported within several days of the first releases and by the end of the winter fishery in Area J in 1971, 404 tags were recovered (Fig. 5B). The next tag recaptures were from St. George's Bay (at least three) in April and from the Bird Rocks area (at least four) in April-May. The subsequent summer fishery in the southern Gulf yielded 15 tags mainly from the American Bank-Gaspé area. The 1971-72 winter fishery in Area J yielded 18 tags and subsequent returns were received from St. George's Bay (two tags) in the spring of 1972, from the 1972 Area T summer fishery (15 tags) and from the 1973 spring fishery in St. George's Bay (two tags only). Total recaptures from the 1971 liberations to the end of May 1973, were 467 tags, a recovery percentage of 4.65%.

The complementary tagging experiments in the southern Gulf confirmed and provided additional information on the migration patterns indicated by the Newfoundland releases. Tag returns from the Magdalen releases (Table 4) reveal that at least a portion of the Magdalen spring-spawners moved westwards on a post-spawning feeding migration to the American Bank-Bradelle Bank area during the summer (Fig. 5C). Subsequent returns were reported from the eastern tip of Prince Edward Island in October 1970 and from the winter, spring and summer fisheries in Southwest Newfoundland, St. Pauls-Magdalen and Gaspé-Chaleur Bay area respectively during the 1971-73 fishing seasons. Total recaptures from the 1970 Magdalens experiment were 141 tags, a recovery percentage of 0.40%.

Tag returns from the Gaspé tagging experiment (Table 5) confirmed the emigration of autumn-spawning herring from Area T to over-wintering areas along Southwest Newfoundland and also the pattern of immigration to the southern Gulf in late spring (Fig. 5D). Low recoveries in Area J during the 1971-72, 1972-73 winter fisheries were due to a combination of low landings and a decreasing proportion of industrial fish. Total recoveries from the Gaspé releases were 1,104 tags, a recovery percentage of 5.52%.

TABLE 6. Recovery efficiencies and rates of return of tags recovered from seeding experiments in reduction plants along Southwest Newfoundland.

Plant	Date seeded	Number seeded	Tag recoveries after												Total recovered	Recovery efficiency (e) (%)
			1 day		5 days		10 days		20 days		40 days		>40 days			
			No.	%	No.	%	No.	%	No.	%	No.	%	No.	%		
Isle aux Morts	15 Nov. 1969	300	49	48.0	92	90.1	98	96.0	102	100.0	102	100.0	102	100.0	102	34.0
Isle aux Morts	9 Jan. 1971	300	56	38.6	139	95.9	139	95.9	141	97.2	145	100.0	145	100.0	145	48.3
Burgeo	17 Jan. 1971	300	135	51.7	176	67.4	183	70.1	217	83.1	221	84.7	261	100.0	261	87.0

Estimates of tag recovery efficiency

To test the recovery efficiency (e) and rate of tag return from the meal lines of reduction plants seeding experiments were conducted which involved introducing a known number of tagged fish (300) into the plant and recording subsequent recoveries. The results (Table 6) indicate that the reduction plant at Burgeo was considerably more efficient in recovering tags than the Isle aux Morts plant although the rate of tag returns was substantially less. Within 5 days over 90% of the total tag recoveries had been recovered by the Isle aux Morts plant and within 10 days this had increased to 96% whereas at the Burgeo plant the recovery rates after 5 and 10 days were 67.4% and 70.1% respectively. The increase in recovery efficiency of the Isle aux Morts plant from 1969 to 1971 was due to the installation of a second magnet located after the fish boilers.

$$\hat{N} = \frac{M(C+1)}{R+1} = \frac{17,000 \times 10,520}{701} = 255,000 \text{ tons}$$

The rate of exploitation from landing and tag recapture data at the Isle aux Morts reduction plant for the last month of the fishery is therefore:

$$\hat{\mu} = \frac{R}{M} = \frac{700}{17,000} = 4.12\%$$

The 95% fiducial limits for $\hat{\mu}$ are 3.83–4.41% and for the effective number of tag recaptures (R) are 651–750. By substituting these latter values for R + 1 in the population size equation, the 95% fiducial limits for N are estimated as 238,000–275,000 tons. Since the estimates of tagging mortality and tag recovery efficiency have a certain variance which is not taken into account in the above confidence limits, the variances of $\hat{\mu}$ and \hat{N} are underestimated.

Biomass estimates of Area T herring over-wintering in Area J

The stock size of over-wintering in Southwest Newfoundland at the time of the 1970 taggings has been estimated from tags recaptured from that experiment during the remainder of the winter fishery in that area (mid-March to mid-April). Only tag recaptures from the Isle aux Morts plant have been used in the population estimates mainly because the bulk of the catches were landed there and also an estimate of the recovery efficiency was available for that plant. Estimates of initial tagging mortality and effective number of herring tagged are available from Winters (1975). Thus for the 1970 returns from Isle aux Morts we have the following information:

Number of tags released (N)	25,000
Initial tagging mortality (A)	0.32
Number of fish effectively tagged (M)=N(1-A) ...	17,000
Landings 13 March–15 April 1970 (C)	10,520 tons
Number of tags recaptured (r)	238
Tag recovery efficiency (e)	0.34
Effective number of tag recaptures (=r/e)(R)	700

The population size of the Southwest Newfoundland population of herring at the time of the March 1970 taggings is therefore estimated as:

The total landings from the winter fishery along Southwest Newfoundland prior to 13 March 1970, were 127,000 tons. Thus, the stock strength at the start of the 1969–70 winter fishery is estimated to be in the range of 387,000–426,000 tons, including adjustment for natural mortality.

The stock sizes supporting the 1971 winter fishery have been estimated from recaptures resulting from both the January 1971 liberations at Bay de Loup and the 1970 releases along Southwest Newfoundland. There were substantial landings and tag recaptures from both the Isle aux Morts and the Burgeo reduction plants during 1971 and thus estimates of the population parameters were derived from the combined recapture data accruing from these plants. For the 1971 tagging experiment we have the following information:

Combined landings 28 January–15 April 1971 (C)	28,700 tons
Number of fish effectively tagged (M)	5,450
Effective number of tag recaptures (R)	649

The population size of over-wintering herring along Southwest Newfoundland at the time of the Bay de Loup

tagging is therefore estimated as:

$$\hat{N} = \frac{M(C + 1)}{R + 1} = \frac{5450 \times 28,700}{650} = 241,000 \text{ tons}$$

The rate of exploitation for the period under consideration based on landings at Isle aux Morts and Burgeo is estimated as:

$$\hat{\mu} = \frac{R}{M} = \frac{649}{5,450} = 11.91\%$$

The 95% fiducial limits for $\hat{\mu}$ are 11.47-12.35%. Multiplying these by 5450 the limits of confidence for the effective number of recaptures are 625-673 which represent a stock size range of 232,000-250,000 tons.

The total landings from the 1970-71 winter fishery prior to 28 January 1971 were 49,000 tons. Consequently the population size at the beginning of the 1970-71 winter fishery including adjustment for natural mortality is estimated from the 1971 tagging experiment in the range of 287,000-314,000 tons.

The stock size of herring at the beginning of the 1971 winter fishery along Southwest Newfoundland may also be estimated from returns from that fishery of fish tagged during the 1970 experiment in that area providing an estimate of the number of the 1970 tagged fish which survived to the beginning of the 1971 winter fishery is available. Such an estimate is available from Winters (1975).

Thus for the 1970 tagging experiment we have the following information from the 1971 winter fishery in Area J:

Combined landings, November-April (C) ..	104,000 tons
Number of surviving tagged fish (M)	389
Effective number of tag recaptures (R)	186

The population size of over-wintering herring in Area J at the beginning of the 1971 winter fishery can therefore be calculated from the returns of the 1970 experiment as follows:

$$\hat{N} = \frac{M(C + 1)}{R + 1} = \frac{389 + 104,000}{187} = 218,000 \text{ tons}$$

The rate of exploitation for the 1971 winter fishery along Southwest Newfoundland is estimated as:

$$\hat{\mu} = \frac{R}{M} = \frac{186}{389} = 47.6\%$$

The 95% fiducial limits for $\hat{\mu}$ are 42.6-52.6% which represents a stock size range of 197,000-244,000 tons. Estimates of stock size at the beginning of the 1971 winter fishery in Area J from both tagging experiments range from 197,000 to 314,000 tons with a mean estimate of 259,000 tons.

Discussions and Conclusions

The returns from both the 1970 and 1971 tagging experiments show that in early April there is an exodus of herring from Southwest Newfoundland around Cape Ray and eventually by early May a movement westwards across Cabot Strait onto the Magdalens Shelf area. Since spring-spawning of herring occurs extensively around the Magdalens it is reasonable to conclude that at least some of the spring-spawners separate from the main migrating stock at this time and move inshore and spawn. The remainder, consisting of a mixture of spring- and autumn-spawners move westwards into the southern Gulf by way of the Bird Rocks. In late June some of these herring inhabit the American Bank area which is a major feeding area for herring and by July are dispersed around the Gaspé-Chaleur Bay area where extensive spawning occurs in late summer and early autumn.

Emigration from the southern Gulf begins in October and it appears that at least some herring move southwards towards Prince Edward Island before moving eastwards towards the Bird Rocks area in November. Hodder and Parsons (1971) have analyzed various biological characteristics of herring from the Bird Rocks in November and have concluded on the basis of length, age, maturity and meristic similarities that these are southern Gulf herring enroute to an over-wintering area along Southwest Newfoundland. Since the first significant catches in Southwest Newfoundland occur around early December (Hodder, 1970) the eastward migration across Cabot Strait probably occurs in late November.

Thus the results of the above tagging experiments confirm Hodder's (1969) hypothesis that the herring which support the winter fishery along Southwest Newfoundland are not indigenous to that area but rather represent the over-wintering phase of a stock complex of herring derived from spring- and autumn-spawnings in the southern Gulf of St. Lawrence. The most significant implication of such a conclusion is that the mobile fleet fisheries which developed in Areas T and J in the late 1960's and the associated over-capitalization of boats and processing facilities were based not on different stocks but rather on one southern Gulf stock complex which was fished at different times and placed along its seasonal migration route. The southern Gulf stock complex of herring was

therefore being exploited almost year-round; this fact alone increased the probability that fishery induced mortality contributed significantly to the sharp decline in herring landings in recent years (Winters and Hodder, 1975).

The estimated stock size of herring along Southwest Newfoundland declined from an average of 407,000 tons in the autumn of 1969 to 259,000 tons in 1970, a reduction of about 36%. Over the same period cohort analyses (Winters and Hodder, 1975) of the total stock complex (Areas T and J) indicates a decline of 30%. Adjusted catch-per-unit-effort in Area J dropped 31% from 41.5 tons per day in 1969-70 to 24.5 tons per day in 1970-71 (Winters and Hodder, 1975) whereas catches dropped only 26% from 140,000 tons in 1969-70 to 104,000 tons in 1970-71. This lesser drop in catch probably occurred as a result of a small increase in the exploitation rate from 34% in 1969-70 to about 40% in 1970-71.

Of additional significance in understanding the overall abundance changes is the fact that over-wintering herring are shown by the earlier analysis of the tag returns to be exploited intensively in the southern Gulf of St. Lawrence during the summer period. Despite an apparent increase in fishing effort in Area T (Winters and Hodder, 1975), Gulf herring landings dropped from 176,000 tons in 1970 and 131,000 tons in 1971, a decline of almost the same proportion as the Newfoundland landings, which substantiates the decline in abundance by analysis of tag recaptures. In addition, the relatively higher landings in Area T compared to Area J in 1970 and 1971 on the same migrating Gulf stock which was subject to seasonal exploitation rates of 34-40% in Area J, confirms the results of cohort analyses (Winters and Hodder, 1975) that the annual rate of exploitation of the southern Gulf of St. Lawrence stock complex of herring was in excess of 50% during the early 1970's.

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An Analysis of Some Factors Affecting the Catchability of Fish by Bottom Trawls

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Abstract

The data from 515 comparative tows by the research vessels *Albatross IV* and *Belogorsk* using the Yankee No. 36 and the modified Yankee No. 41 bottom trawls during day and night were analyzed for 23 species groups (including all species together). In general, demersal species were significantly more vulnerable to trawl gear during night than during day, while the converse was true for semi-pelagic species. The fishing power of the No. 41 trawl was significantly greater (and never significantly lower) than the fishing power of the No. 36 trawl for 15 of the 23 species groups. The relative fishing power of the trawls was significantly affected by the towing vessel for six of the species groups.

Introduction

Research bottom-trawl surveys along the Northwest Atlantic coast of the USA are intended to provide an index of abundance of species of the region. Catch per unit of fishing effort in these surveys is affected by the catchability¹ of fish by the fishing gear being used and also by the density of the fish in the area sampled. Therefore, the fishing power (relative catchability of fish) of the two trawls predominantly used by research vessels in the area was estimated so as to allow comparison between survey results using either of these gears.

The fishing power of a trawl depends on the towing vessel (size, power, speed, etc.), physical factors (light conditions, sea state, bottom type, currents, etc.) and trawl design. The factorial experiment described below provided an adequate set of data to estimate the fishing power of both trawls when towed by two vessels of different sizes during periods of daylight and darkness.

USA autumn bottom-trawl surveys were initiated in 1963 using the No. 36 Yankee trawl. Spring bottom-trawl surveys were begun in 1968 using the same gear, but a modified Yankee No. 41 high-opening trawl has been used since 1973. A detailed description of the trawls is given by Bowman (MS 1976) along with some of the reasons for changing from the No. 36 trawl to the larger modified No. 41 trawl. Grosslein (1969) described the methodology of the USA bottom-trawl surveys.

Gear Comparison Experiment

Gear comparison studies were conducted during the autumn of 1973-75 using the research vessels *Albatross IV* and *Belogorsk*. The *Albatross IV* [56 m in length, 853 gross tons (metric), 1,000 horsepower] is operated by the National Oceanic and Atmospheric Administration and assigned to the Northeast Fisheries Center of the National Marine Fisheries Service, USA. The *Belogorsk* (69 m, 2,213 gross tons, 1,600 horsepower) is operated by the Atlantic Research Institute of Marine Fisheries and Oceanography (AtlantNIRO), Kaliningrad, USSR.

The vessels operated simultaneously at randomly selected locations within a 65-km² area. All tow locations were in waters south of Martha's Vineyard centered at 40°50'N and 70°20'W during 1973-74 but in 1975 about half of the tows were made on the southern part of Georges Bank centered at 41°24'N and 66°53'W, with the other half at the previous location. The order in which the two gears were towed was also selected randomly. The towing speed was about 6.4 km per hour. The direction of towing was toward the next randomly selected station. Tows were made with all combinations of ship and gear during day and night periods (dawn and dusk excluded). Data from 32 days of gear comparison studies are considered in this paper. Sixteen tows (2 gears × 2 vessels × 2 time periods × 2 replicates) were planned for each of the first 30 days of the experiment and 24 tows were implemented during the last 2 days of the experiment by increasing the number of

¹ Catchability is defined as the fraction of a fish population which is caught by a defined unit of fishing effort (Ricker, 1975). The unit of fishing effort considered in this paper is one 30-min tow. The term "vulnerability" is equivalent to catchability but is usually applied to separate parts of a population such as particular size categories.

replicates to three. During the experiment 13 tows were not completed or were disregarded because of factors beyond the control of the experimenters. Therefore the results of this paper are based on 515 tows ($30 \times 16 + 2 \times 24 - 13$). A more complete account of the gear comparison experiments is given by Bowman (MS 1976).

Method of Analysis

Using the approach of Robson (1966), the following model was applied to the data from gear comparison experiments:

$$C = \alpha_i \beta_j \gamma_k (\alpha\beta)_{ij} (\alpha\gamma)_{ik} (\beta\gamma)_{jk} \phi P \bar{\epsilon} \quad (1)$$

where C is catch per tow; P is population density; ϕ is the catchability coefficient under standard conditions (to be defined); $\bar{\epsilon}$ is a log-normally distributed random variable; α_i , β_j and γ_k are multiplicative gear, diel and ship factors respectively; $(\alpha\beta)_{ij}$, $(\alpha\gamma)_{ik}$, and $(\beta\gamma)_{jk}$ are multiplicative gear-diel, gear-ship, and diel-ship interaction factors respectively.

Fishing with the No. 36 Yankee trawl by the *Albatross IV* during daylight was arbitrarily chosen as the standard situation, and therefore α_1 (No. 36 trawl), β_1 (day period) and γ_1 (*Albatross IV*) all equal 1.0. The interaction terms also equal 1.0 unless both subscripts are 2. The goal of the analysis is to estimate α_2 (No. 41 trawl), β_2 (night period), γ_2 (*Belogorsk*), $(\alpha\beta)_{22}$ (No. 41 trawl-night period interaction), $(\alpha\gamma)_{22}$ (No. 41 trawl-*Belogorsk* interaction), and $(\beta\gamma)_{22}$ (night period-*Belogorsk* interaction).

Since population size is unknown, fluctuations in P cannot be accounted for directly in the model. An alternate approach (in the absence of a measure of population abundance) is to compare C for various combinations of gear, ship, and light level within the same day of the experiment, assuming that the size of the population being sampled (within the 65-km² sample area) is relatively constant over a brief time interval. Following this approach, P is replaced by $\psi_1 \bar{P}$ where \bar{P} is the average population size over all days of the experiment and ψ_1 is the ratio of P for day 1 to \bar{P} . The product of \bar{P} and ϕ can be replaced by θ . Therefore, making the substitutions and taking the natural logarithm (ln) of both sides of Equation (1):

$$\begin{aligned} \ln C &= \ln \alpha_i + \ln \beta_j + \ln \gamma_k + \ln (\alpha\beta)_{ij} \\ &+ \ln (\alpha\gamma)_{ik} + \ln (\beta\gamma)_{jk} + \ln \theta \\ &+ \ln \psi_1 + \ln \bar{\epsilon} \end{aligned} \quad (2)$$

where 1 ranges from 1 to 32, and i, j and k each equals 1 or 2. Using the convention $X' = \ln X$ for any symbol X, and rewriting Equation (2) as a multiple linear regression problem with dummy variables,

$$\begin{aligned} C' &= \theta' + \alpha' X_1 + \beta' X_2 + \gamma' X_3 + (\gamma\beta)' (X_1 X_2) \\ &+ (\alpha\gamma)' (X_1 X_3) + (\beta\gamma)' (X_2 X_3) \\ &+ \sum_{m=1}^{31} \psi_m X_{m+3} + \epsilon' \end{aligned} \quad (3)$$

$$\text{where } X_1 = \begin{cases} 0 & \text{for No. 36 trawl} \\ 1 & \text{for No. 41 trawl} \end{cases}$$

$$X_2 = \begin{cases} 0 & \text{for daylight} \\ 1 & \text{for darkness} \end{cases}$$

$$X_3 = \begin{cases} 0 & \text{for } Albatross IV \\ 1 & \text{for } Belogorsk \end{cases} \quad (4)$$

$$X_{m+3} = \begin{cases} 1 & \text{for day } m \\ -1 & \text{for day } 32 \\ 0 & \text{for otherwise} \end{cases}$$

and ϵ' is normally distributed.

The number of dummy variables used for each factor (gear, diel, ship and day) is one less than the number of levels of that factor. This is necessary so that the design matrix of the model is non-singular and thus invertible, allowing the parameters of Equation (3) to be estimated. For the gear, diel and ship factors, the number of parameters and dummy variables is reduced to 1 (thus the subscripts of α' , β' and γ' are dropped), by assuming a standard and only estimating departures from the standard. For the day factor, ψ_m is considered a departure from the average condition over all days of the experiment, and therefore

$$\sum_{m=1}^{32} \psi_m' = 0 \quad \text{or} \quad \psi_{32}' = - \sum_{m=1}^{31} \psi_m' \quad (5)$$

The designation of dummy variable in Equation Set (4) is equivalent to Equation (5).

The parameters of Equation (3) were estimated by stepwise multiple regression using the Statistical Package for the Social Sciences (SPSS) (Nie *et al.*, 1975). Independent variables were only included in Equation (3) if they reduced enough residual variance to be statistically significant at the 5% level. The analysis was conducted for

species caught in significant amounts during the experimental tows and for all species together with the catch expressed in numbers and weight. Data for some species were analyzed because of commercial and recreational interests, even though they were a minor component of the catch.

In practice, the catch of all of the species considered was 0 for some of the 515 tows, so that the $\ln C$ was sometimes undefined. This problem is usually avoided by adding 1.0 to C , resulting in C' greater than or equal to 0. While it is necessary to add some constant to C when the parameters to be estimated are ratios, the parameter estimates are affected by the constant which is added. This is especially true when C is the same order of magnitude as the constant that is added to it. For example, the ratio of 2 to 4 is substantially different from the ratio of 3 to 5. Therefore, 0.1 was added to C to assure that C' was always defined, while minimizing the distortion of parameter estimates. A smaller value than 0.1 was not used because this would have had an undesirable effect on the residuals from regression as will be discussed later.

Let \hat{X}' be an unbiased estimate of X' with a normal distribution. The antilogarithm of \hat{X}' (where $X' = \ln X$) is a biased estimate of X since the expected value of $e^{\hat{X}'}$ is

$$E(\hat{X}') = e^{X' + \sigma^2/2} = X e^{\sigma^2/2} \quad (6)$$

where σ is the variance of \hat{X}' (Brownlee, 1965). Therefore

$$E(e^{\hat{X}' - \sigma^2/2}) = X \quad (7)$$

is an unbiased estimator. Since σ^2 is estimated by s^2 , an approximately unbiased estimate of X is obtained by taking the antilogarithm of $\hat{X}' - s^2/2$. This method was used to estimate α , β , γ , $(\alpha\beta)$, $(\alpha\gamma)$ and $(\beta\gamma)$ from the regression coefficients estimated for Equation (3). The 95% confidence intervals of these coefficients were obtained by taking the antilogarithm of the end points of the 95% confidence intervals of α' , β' , γ' , $(\alpha\beta)'$, $(\alpha\gamma)'$ and $(\beta\gamma)'$.

Results

About 85 species were caught in the 515 tows considered in this paper. Of these, 22 species groups (or species), which comprised 91% of the total catch, were analyzed as described in the previous section. The analysis was also applied to the catch of all species combined. The mean catch per tow in weight and numbers by species group for each cell of the experiment

(combination of gear, diel and ship factors) is given in Table 1. Since the number of observations is nearly equal for each cell, the mean catch over several cells can be approximated by averaging values available in Table 1.

Statistically significant (at the 5% level)² estimates of the parameters of Equation (1) are given in Table 2. The 95% confidence limit of these estimates (labeled as minimum and maximum estimate) and the percentage of the variation in transformed catch explained by Equation (3) are also given in Table 2. Some of the reduction in variability is attributed to the ψ terms of the model, but these are not reported in the table because they are only applicable to fishing at a specific location on a particular day in the past.

The estimates in Table 2 are based on the assumption that ϵ' [of Equation (3)] is an independent (not auto-correlated) normally distributed random variable with a constant variance at all levels of C' . Parameter estimates of Equation (3) are the minimum variance linear (linear function of set of C') unbiased estimates even for a non-normal distribution of ϵ' (Gauss-Markoff theorem; see Graybill, 1961). Furthermore, tests of significance and confidence intervals are robust when ϵ' has a non-normal distribution and linear models are particularly robust to non-normal residuals and a non-constant variance when the number of observations in each cell is equal (Scheffe, 1963). The number of observations in each cell of this analysis is nearly equal.

A test for autocorrelation of residuals from a regression equation was derived by Durbin and Watson (1951). The Durbin and Watson test statistic (d) has an expected value of 2.0, with lower values indicating positive autocorrelation and higher values indicating negative autocorrelation. An exact test of the significance of d is not available, but an approximate test is provided by Durbin and Watson for up to 100 observations and five independent variables. The regression equations, on which Table 2 is based, are for 515 observations and usually more than 10 independent variables. Extrapolating from the work of Durbin and Watson (1951; their table 5), a significant (5% level) degree of autocorrelation appears indicated for $d < 1.5$ or $d > 2.5$. The Durbin and Watson statistic for each regression equation is given in Table 2. Based on these statistics, it appears that residuals tend to be positively autocorrelated (only 6 of 48 are greater than 2.0) but individual values of d seldom appear significant at the 5% level. This tendency for residuals to be mildly autocorrelated probably results in little underestimation of the width of confidence intervals because of the large number of degrees of freedom associated with the analysis.

The residuals from each regression equation were examined visually in order to detect violations of the

² Significance levels are probably slightly exaggerated when coefficients of a linear model are fit by stepwise multiple regression. For the same reason, the width of confidence intervals is probably slightly underestimated.

TABLE 1. Mean catch per tow. (A) in weight in centigrams (100 g); and (B) in numbers.

	Albatross IV				Belogorsk				Species mean	% of tows present
	Day		Night		Day		Night			
	No. 36	No. 41	No. 36	No. 41	No. 36	No. 41	No. 36	No. 41		
(A) Bluefish, <i>Pomatomus saltatrix</i>	35.2	35.2	16.0	4.3	22.5	43.4	5.5	3.9	20.6	29
Butterfish, <i>Poronotus triacanthus</i>	99.7	132.3	2.9	7.3	68.5	71.0	1.8	4.8	48.2	71
Cancer crabs, <i>Cancer</i> spp.	5.3	10.7	4.9	10.9	0.1	20.8	0.1	26.7	9.9	60
Dogfish, <i>Mustelus canis</i> and <i>Squalus acanthias</i>	36.3	157.7	48.1	80.0	67.8	81.6	44.0	68.0	72.6	59
Flounder, 4-spot, <i>Paralichthys oblongus</i>	1.5	3.8	59.6	67.3	0.6	5.6	32.2	72.3	30.5	73
Sand, <i>Scophthalmus aquosus</i>	0.8	1.3	27.9	19.3	0.5	1.4	14.3	24.8	11.3	52
Summer, <i>Paralichthys dentatus</i>	9.4	14.3	7.2	8.1	9.7	18.6	2.6	5.8	9.4	18
Winter, <i>Pseudopleuronectes americanus</i>	10.5	18.8	33.4	35.4	8.8	18.1	16.6	56.6	24.8	77
Yellowtail, <i>Limanda ferruginea</i>	11.7	16.9	60.1	63.3	5.9	13.3	29.7	77.4	34.9	85
Goosefish, <i>Lophius americanus</i>	13.0	21.0	21.4	49.5	5.9	24.2	14.7	58.2	26.0	43
Hake, Red, <i>Urophycis chuss</i>	0.0	0.8	10.2	7.5	0.1	0.5	8.5	8.1	4.5	34
Silver, <i>Merluccius bilinearis</i>	13.0	22.3	41.0	180.0	9.8	23.5	18.6	158.8	58.6	84
Herring, Round, <i>Etrumeus sadina</i>	54.0	38.8	0.0	0.3	76.2	60.3	0.1	0.0	28.2	24
Lobster, <i>Homarus americanus</i>	9.4	22.8	8.7	18.3	10.1	20.3	7.6	22.5	14.9	58
Sculpin, Longhorn, <i>Myoxocephalus octodecemspinosus</i>	0.3	0.6	10.6	18.8	0.4	0.6	12.9	22.2	8.3	39
Scup, <i>Stenotomus chrysops</i>	16.5	9.7	17.7	27.9	10.4	15.7	8.4	18.3	15.6	61
Sea raven, <i>Hemitripteris americanus</i>	1.5	1.9	3.9	6.4	1.3	2.5	2.6	6.7	3.4	23
Sea robin, Common, <i>Prionotus carolinus</i>	0.1	0.2	8.3	6.6	0.1	0.1	2.9	6.6	3.1	28
Skate, Big, <i>Raja ocellata</i>	2.2	3.4	11.0	4.0	3.1	6.8	23.6	34.3	11.0	19
Little, <i>Raja erinacea</i>	15.4	31.5	147.3	237.0	10.9	44.8	71.6	383.0	117.9	86
Squid, <i>Illex illecebrosus</i>	1.6	2.4	1.2	1.6	1.1	1.2	1.6	1.4	1.5	32
<i>Loligo pealei</i>	272.6	275.8	50.0	34.6	157.5	293.8	42.8	43.5	145.1	74
All species	655.8	913.6	596.2	895.7	638.0	1,012.2	375.2	1,118.7	771.7	100
(B) Bluefish, <i>Pomatomus saltatrix</i>	1.0	1.1	0.5	0.1	0.7	5.6	0.2	0.1	1.1	29
Butterfish, <i>Poronotus triacanthus</i>	304.5	420.0	10.3	15.5	197.5	279.6	6.7	11.5	155.0	71
Cancer crabs, <i>Cancer</i> spp.	6.9	13.6	7.1	11.4	0.1	19.7	0.2	30.8	11.2	60
Dogfish, <i>Mustelus canis</i> and <i>Squalus acanthias</i>	5.2	56.5	8.1	22.2	23.7	18.0	5.0	11.6	18.8	59
Flounder, 4-spot, <i>Paralichthys oblongus</i>	0.8	2.1	33.3	36.2	0.4	2.5	17.8	41.1	17.0	73
Sand, <i>Scophthalmus aquosus</i>	0.3	0.6	12.2	7.8	0.1	0.7	5.3	11.1	4.8	52
Summer, <i>Paralichthys dentatus</i>	0.4	0.6	0.4	0.4	0.3	0.8	0.1	0.4	0.4	18
Winter, <i>Pseudopleuronectes americanus</i>	3.0	5.6	11.2	11.5	2.7	6.2	5.4	19.8	8.2	77
Yellowtail, <i>Limanda ferruginea</i>	4.5	6.7	25.6	26.1	2.3	5.7	11.7	34.8	14.8	85
Goosefish, <i>Lophius americanus</i>	0.4	1.0	1.1	1.9	0.2	0.9	0.4	2.5	1.0	43
Hake, Red, <i>Urophycis chuss</i>	0.2	0.5	11.6	7.1	0.1	0.4	8.8	8.1	4.6	34
Silver, <i>Merluccius bilinearis</i>	9.5	18.1	112.4	303.5	13.6	21.4	82.6	296.4	108.1	84
Herring, Round, <i>Etrumeus sadina</i>	156.2	140.2	0.1	0.5	211.4	314.2	0.4	0.1	101.0	24
Lobster, <i>Homarus americanus</i>	1.4	2.7	1.0	3.1	1.3	3.2	0.7	2.6	2.0	58
Sculpin, Longhorn, <i>Myoxocephalus octodecemspinosus</i>	0.2	0.5	9.8	15.7	0.1	0.5	11.3	19.3	7.2	39
Scup, <i>Stenotomus chrysops</i>	8.7	4.8	17.4	16.4	4.7	7.8	5.8	14.0	10.0	61
Sea raven, <i>Hemitripteris americanus</i>	0.2	0.4	0.8	1.4	0.3	0.4	0.8	1.8	0.8	23
Sea robin, Common, <i>Prionotus carolinus</i>	0.1	0.2	4.0	3.2	0.1	0.1	1.7	3.6	1.7	28
Skate, Big, <i>Raja ocellata</i>	0.2	0.3	1.9	0.4	0.2	1.1	3.9	5.4	1.7	19
Little, <i>Raja erinacea</i>	3.0	7.0	29.9	54.4	2.0	9.5	14.4	85.8	25.9	86
Squid, <i>Illex illecebrosus</i>	3.7	3.3	0.6	0.9	2.8	1.9	0.8	0.8	1.8	32
<i>Loligo pealei</i>	3,193.1	2,368.8	144.2	113.9	2,751.7	3,652.5	218.9	170.1	1,560.6	74
All species	4,475.8	3,633.5	455.6	667.7	5,985.0	6,518.7	414.8	788.4	2,830.7	100

assumption of a constant variance and normal distribution. The range of residuals about the expected transformed catch (C') appears independent of the level of C' , and thus there is no evidence that the assumption of a constant variance is violated.

Two examples of the distribution of residuals from regression equations reported in this paper are given in Fig. 1 and 2, which indicate that the distribution is truncated in the lower left quadrant. This occurs because the lowest possible value of C' is $-2.30 (\ln 0.1)$ which corresponds to a species being absent from a tow. Therefore, all observations of zero catch fall on the straight line described by: Residual = $-2.30 - \text{Expected } (C')$. When a species is absent from a substantial number of tows, the

distribution of residuals looks particularly abnormal because so many observations lie along this line. While the robustness of the regression model is probably adequate to allow residual distribution with some irregularities (such as Fig. 1), the abnormality in Fig. 2 casts doubt on parameter estimates and particularly on confidence limits. Species for which residuals have an extremely abnormal appearance are indicated in Table 2 by an asterisk. In general, these species were absent from 50% or more of the tows.

The abnormal appearance of residuals could have been reduced by using the $\ln (C + 1.0)$ transformation instead of $\ln (C + 0.1)$, since the gap between a catch of 0 and 1 fish in a tow is much smaller for the former than the

TABLE 2. Fishing power coefficients estimated by fitting Equation (3) and retransforming parameters by Equation (7). Minimum and maximum estimates indicate endpoints of 95% confidence intervals.

Species		α			β			γ			$(\alpha\beta)$			$(\alpha\gamma)$			$(\beta\gamma)$			% SS reduced	Durbin-Watson Statist.
		Min. est.	Max. est.	est.	Min. est.	Max. est.	est.	Min. est.	Max. est.	est.	Min. est.	Max. est.	est.	Min. est.	Max. est.	est.	Min. est.	Max. est.	est.		
Bluefish *	Number	--	--	--	0.29	0.36	0.44	--	--	--	--	--	--	--	--	--	--	--	18.1	1.92	
	Weight	--	--	--	0.14	0.19	0.27	--	--	--	--	--	--	--	--	--	--	--	18.0	1.92	
Butterfish	Number	--	--	--	0.048	0.06	0.09	0.52	0.70	0.97	--	--	--	--	--	--	--	--	71.2	1.60	
	Weight	1.05	1.35	1.78	0.084	0.11	0.14	0.50	0.64	0.84	--	--	--	--	--	--	--	--	60.0	1.66	
Cancer crabs	Number	3.92	5.72	8.70	--	--	--	0.12	0.18	0.53	--	--	--	10.80	18.31	33.80	--	--	56.0	1.30	
	Weight	2.60	3.59	5.10	--	--	--	0.27	0.37	0.53	--	--	--	4.29	6.73	11.20	--	--	44.0	1.18	
Dogfish	Number	1.07	1.40	1.88	--	--	--	--	--	--	--	--	--	--	--	--	--	--	48.1	1.66	
	Weight	1.03	1.45	2.11	--	--	--	--	--	--	--	--	--	--	--	--	--	--	37.2	1.76	
Flounder 4-spot	Number	1.23	1.63	2.22	32.11	39.42	48.95	0.39	0.52	0.77	--	--	--	1.29	1.92	3.00	--	--	74.5	1.64	
	Weight	1.15	1.48	1.95	26.05	31.35	38.10	0.46	0.59	0.78	--	--	--	1.31	1.89	2.81	--	--	75.6	1.61	
Sand	Number	1.31	1.67	2.15	8.96	11.38	14.69	--	--	--	--	--	--	--	--	--	--	--	52.6	1.67	
	Weight	1.10	1.37	1.74	7.07	8.84	11.21	--	--	--	--	--	--	--	--	--	--	--	50.8	1.67	
Summer *	Number	1.06	1.23	1.42	--	--	--	--	--	--	--	--	--	--	--	--	--	--	50.1	2.11	
	Weight	1.06	1.31	1.64	--	--	--	--	--	--	--	--	--	--	--	--	--	--	47.7	2.13	
Winter	Number	1.63	2.02	2.55	2.61	3.25	4.10	--	--	--	--	--	--	--	--	--	--	--	58.9	1.67	
	Weight	1.32	1.86	2.70	1.98	2.78	4.04	--	--	--	--	--	--	--	--	--	--	--	46.7	1.69	
Yellowtail	Number	1.31	1.76	2.41	4.58	5.66	7.08	0.40	0.54	0.74	--	--	--	1.25	1.88	2.98	--	--	60.5	1.82	
	Weight	1.28	1.73	2.42	3.57	4.45	5.63	0.37	0.51	0.71	--	--	--	1.28	1.97	3.20	--	--	60.2	1.86	
Goosefish *	Number	1.97	2.45	3.08	1.45	1.80	2.27	--	--	--	--	--	--	--	--	--	--	--	30.6	1.85	
	Weight	2.38	3.35	4.86	1.51	2.12	3.07	--	--	--	--	--	--	--	--	--	--	--	20.4	1.79	
Hake Red *	Number	--	--	--	4.42	5.56	7.09	--	--	--	--	--	--	--	--	--	--	--	55.8	1.52	
	Weight	--	--	--	2.35	2.84	3.46	--	--	--	--	--	--	--	--	--	--	--	39.9	1.62	
Silver	Number	1.53	2.36	3.85	11.32	15.53	21.91	0.26	0.41	0.67	--	--	--	1.18	2.15	4.41	--	--	50.0	1.48	
	Weight	1.06	1.61	2.60	2.24	3.18	4.68	0.33	0.47	0.69	1.66	2.69	4.70	1.15	1.86	3.25	--	--	55.1	1.64	
Herring, round *	Number	--	--	--	0.11	0.16	0.23	--	--	--	--	--	--	--	--	--	--	--	32.3	1.56	
	Weight	--	--	--	0.32	0.41	0.52	--	--	--	--	--	--	--	--	--	--	--	20.6	1.65	
Lobster	Number	2.12	2.66	3.37	--	--	--	--	--	--	--	--	--	--	--	--	--	--	39.3	2.01	
	Weight	2.05	2.72	3.70	--	--	--	--	--	--	--	--	--	--	--	--	--	--	27.2	2.02	
Sculpin, Longhorn *	Number	1.29	1.61	2.04	8.03	10.05	12.76	--	--	--	--	--	--	--	--	--	--	--	65.0	1.75	
	Weight	1.13	1.34	1.61	3.38	4.08	4.96	--	--	--	--	--	--	--	--	--	--	--	57.0	1.68	
Scup	Number	--	--	--	1.67	2.17	2.87	--	--	--	--	--	--	--	--	--	--	--	55.1	1.56	
	Weight	--	--	--	1.53	1.96	2.57	0.35	0.50	0.73	--	--	--	--	--	--	--	--	46.8	1.59	
Sea raven *	Number	1.10	1.28	1.49	1.30	1.50	1.75	--	--	--	--	--	--	1.25	2.02	3.51	--	--	63.0	1.77	
	Weight	1.07	1.25	1.46	1.07	1.24	1.45	--	--	--	--	--	--	--	--	--	--	--	59.0	1.74	
Sea robin *	Number	--	--	--	3.42	4.18	5.17	0.55	0.71	0.92	--	--	--	1.20	1.59	2.16	--	--	47.0	1.54	
	Weight	--	--	--	2.33	2.77	3.32	--	--	--	--	--	--	--	--	--	--	--	37.0	1.50	
Skate Big *	Number	--	--	--	1.08	1.41	1.87	--	--	--	--	--	--	--	--	--	1.10	1.50	2.09	27.6	1.58
	Weight	--	--	--	1.38	1.77	2.30	1.01	1.29	1.68	--	--	--	--	--	--	--	--	79.0	1.74	
Little	Number	3.15	3.98	5.12	8.82	11.16	14.34	--	--	--	--	--	--	--	--	--	--	--	57.7	1.51	
	Weight	3.23	4.14	5.41	9.39	12.05	15.75	--	--	--	--	--	--	--	--	--	--	--	55.1	1.59	
Squid Illex *	Number	--	--	--	0.43	0.58	0.71	--	--	--	--	--	--	--	--	--	--	--	57.9	1.59	
	Weight	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	55.9	2.00	
Loligo	Number	--	--	--	0.04	0.05	0.07	--	--	--	--	--	--	--	--	--	--	--	83.3	1.56	
	Weight	--	--	--	0.25	0.38	0.58	0.25	0.37	0.58	0.35	0.57	0.99	1.22	2.00	3.52	--	--	58.9	1.48	
All species	Number	--	--	--	0.25	0.32	0.42	--	--	--	--	--	--	--	--	--	0.49	0.67	0.94	55.0	1.47
	Weight	1.54	1.86	2.27	--	--	--	--	--	--	1.03	1.28	1.62	1.29	1.77	2.50	--	--	28.0	1.60	

* Extreme violations of underlying assumptions of analysis for these species.

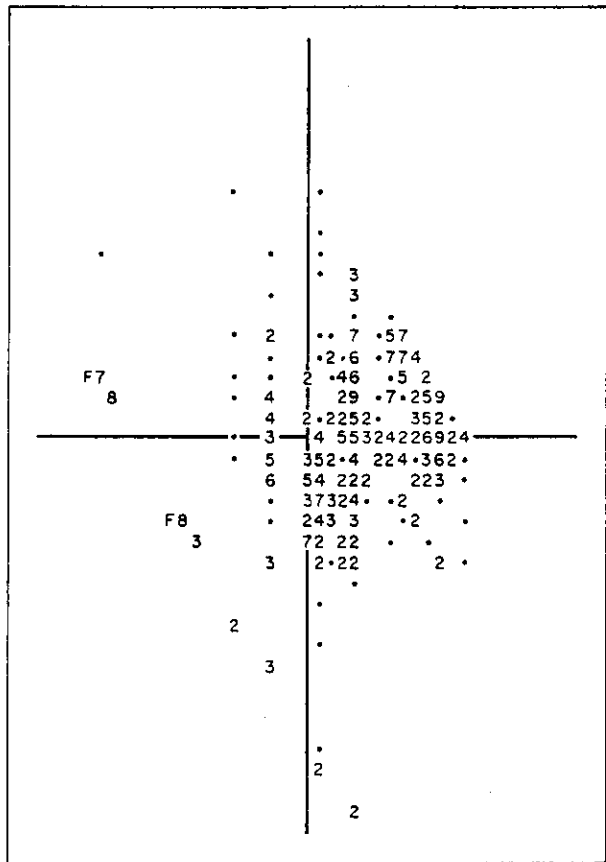


Fig. 1. Residuals (vertical line) versus expected value of C' (horizontal line) for *Loligo*. Numbers indicate number of residuals at approximately the same location on the plot with A, B, C, D, E and F corresponding to 10, 11, 12, 13, 14 and 15 or more residuals.

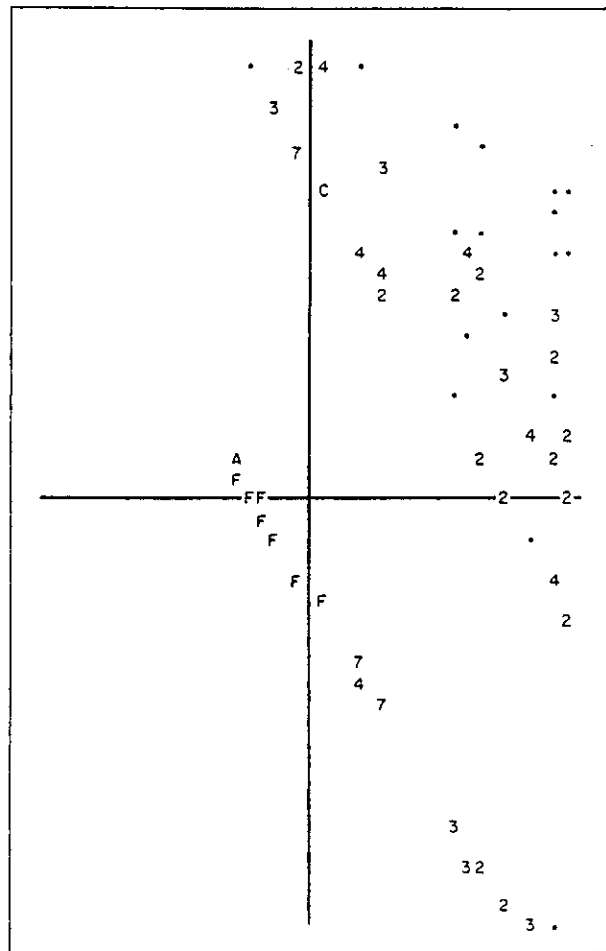


Fig. 2. Residuals (vertical line) versus expected value of C' (horizontal line) for fluke. Numbers indicate number of residuals at approximately the same location on the plot with A, B, C, D, E and F corresponding to 10, 11, 12, 13, 14 and 15 or more residuals.

latter transformation ($\ln 1.1 - \ln 0.1 = 2.4$, $\ln 2.0 - \ln 1.0 = 0.69$). The serious bias that results from using the $\ln(C + 1.0)$ transform for small values of C was noted under the methods section of the paper. The use of a smaller constant than 0.1 in the transformation would result in still further abnormality of residuals (using 0.01, $\ln 1.01 - \ln 0.01 = 4.62$).

Discussion

Significant day-night differences in catch are indicated for 19 of the 23 species groups considered (including all species grouped together). The differences ranged from nearly a 40-fold increase in catch of fourspot flounder (in numbers) to a decrease in catch of *Loligo* (in numbers) by a factor of nearly 20 when comparing night to day. Generally groundfish (flounders, skate, sculpin and others) were more vulnerable to both trawls at night than during the day while the opposite was true of semi-pelagic species (squid, butterfish, round herring and bluefish). Silver hake which are often assumed to be semi-pelagic

were more vulnerable at night as is characteristic of groundfish. The increased vulnerability of groundfish at night may reflect nocturnal prowling and feeding or decreased avoidance, while the increased vulnerability of semi-pelagic species during the day could result from light inhibition which concentrates fish near the bottom. It is noteworthy that lobsters and *Cancer* crabs, which are believed to be more active at night, were equally catchable during day and night. The differences in vulnerability between day and night are seldom affected by the gear and/or the ship involved. Significant diel-gear or diel-ship interactions were only detected for silver hake, *Loligo* and big skate.

The diel factors (β) for some species were substantially different for catch in numbers and in weight, indicating that the vulnerability of fish as a function of weight changes with light level. For *Loligo*, the mean weight of individuals in the catch was seven times greater for night

tows than for day tows, but the mean weight of silver hake was five times greater during day than at night.

Catchability with the No. 41 trawl was significantly higher than with the No. 36 trawl when towed by the *Albatross IV* for 15 of the 23 species groups. The largest gear factor was 5.72 (for catch in numbers of *Cancer* crabs). The gear factors for goosfish and little skate were also larger than 3.0. A gear factor of 1.15 would result from the greater width (at the wings) of the No. 41 if all other factors are equal. Because of the variability of the data considered in this study, factors between 0.80 and 1.20 were unlikely to be detected as being statistically significant at the 5% level.

Catchability with the No. 36 trawl was often lower (8 of 23 species groups) when towed by the *Belogorsk* than when towed by the *Albatross IV*. Catchability with the No. 36 trawl when towed by *Belogorsk* was less than half the catchability of the same net towed by *Albatross IV* for *Cancer* crabs, silver hake, scup and *Loligo*. On the other hand, catchability with the No. 41 trawl was significantly higher when towed by the *Belogorsk* than when towed by the *Albatross IV* for 6 of the 23 species groups, as indicated by gear-ship interaction factors ($\alpha\gamma$). The value of ($\alpha\gamma$) for *Cancer* crabs in numbers caught was 18.31. Other statistically significant values of ($\alpha\gamma$) were about 2. The mechanisms that result in the greater fishing power of the *Albatross IV* than of the *Belogorsk* when towing the No. 36 trawl for several species and the converse relationship when towing the No. 41 trawl are unknown.

The fishing power coefficients estimated here allow comparison of survey results for data collected either during day or night, with the No. 36 or No. 41 trawl, or with the *Albatross IV* or *Belogorsk*. Obviously, when these coefficients are applied, they introduce an unknown amount of additional imprecision. The available data were inadequate for examination of the seasonal variability in fishing power coefficients. Areal variability was examined (between Georges Bank and southern New England). No significant difference between areas was indicated, but the experiment was not intended to address this problem and therefore this result is inconclusive.

Based on the substantial data considered in this

paper, the relative fishing power of two vessels and two bottom trawls during day and night was estimated to within $\pm 1/3$ (at the 5% level) for several species. Due to violations in regression assumptions, a much lesser degree of confidence is realistic for species absent from a majority of tows. The results indicate that, for most species, more variability in catch is explained by diel variations than by gear type or towing vessel and that the fishing power of trawl gears is often dependent on the towing vessel.

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Each Manuscript should have an abstract not to exceed 3% of the length of the text or 200 words whichever is the smaller. For position of the abstract in the manuscript see (e) above. The abstract should summarize the contents and conclusions of the paper, point to new information in the paper and indicate the relevance of the work.

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