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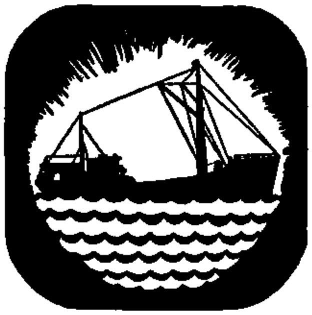

Selected Papers
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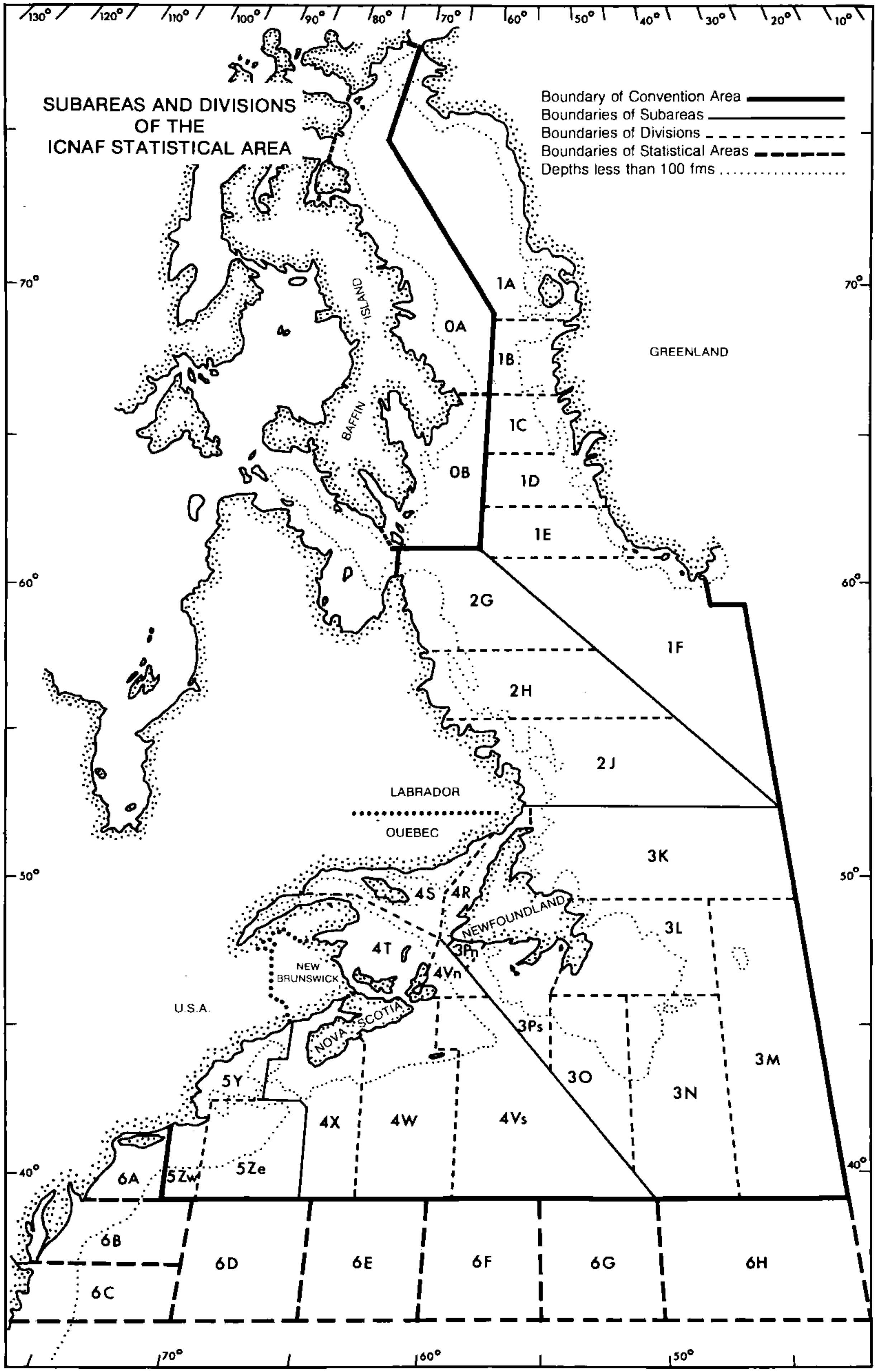
Foreword

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

Papers for publication in this new series are selected, subject to the approval of the authors, by the Steering and Publications Subcommittee of STACRES (Standing Committee on Research and Statistics) from papers presented to scientific meetings of ICNAF. In general, the papers selected contain information which is considered worthy of wider circulation than is normal for meeting documents but not of the standard required for publication in the Research Bulletin series. Each author is supplied with 50 reprints of his or her contribution.



SUBAREAS AND DIVISIONS OF THE ICNAF STATISTICAL AREA

Contents

The Effect of Water Dynamics on Year-Class Strength of Cod on Flemish Cap[1]

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Abstract

The analysis of geostrophic circulation charts based on hydrological data from surveys by USSR research vessels and the International Ice Patrol from 1955 to 1974 indicate the existence of quasi-steady water circulation with anticyclonic motion over the central part of the Flemish Cap. The intensity of the horizontal and vertical water circulation over the central part of the bank during the period of development of cod eggs and larvae was found to be one of the main abiotic factors affecting the abundance of year-classes. It is suggested that these dynamic indices can be used to predict the relative abundance of cod year-classes well in advance of their recruitment to the commercial fishery.

Introduction

It is known that quasi-steady local eddies and circular water motion of comparatively small diameter play an important part in the formation and variation of the physical, chemical and biological properties of water masses and in turn influence the formation of increased biological productivity zones in the ocean. Variability of water convergence on the Flemish Cap significantly affects the survival of pelagic ichthyoplankton and consequently determines the abundance of year-classes of the local cod stock (Kudlo and Borovkov, 1977).

Clockwise water circulation can directly affect the movement of pelagic eggs and larvae from the spawning grounds toward the central part of the bank and the concentration of plankton in the area. The vertical water circulation in the eddy zone regulates the provision of nutrients in the surface layer and consequently the biological productivity of the area.

Materials and Methods

The geostrophic circulation in the Flemish Cap area is based on 15 charts of dynamic topography drawn from temperature and salinity measurements, obtained during hydrological surveys by USSR research vessels (from PINRO) in 1969–74, and on 11 charts drawn from data collected by the International Ice Patrol during 1955–64 (Soule and Murray, 1956, 1957; Soule and Morse, 1958, 1960; Soule and Morrill, 1960; Soule *et al.*, 1961, 1963a, 1963b; Franceschetti *et al.*, 1964; Kollmeyer *et al.*, 1965).

The volume of the total horizontal water transport in the 0–100 m layer (Q_s) along the standard 47°N section (six stations on the Flemish Cap) was taken as the index of degree of development of the anticyclonic water circulation over the top of the bank. This volume was calculated by the dynamic method (Zubov and Mamaev, 1956).

The strength of the vertical water movements over the bank, in terms of the volume of water rising per unit time (Q_w in cm^3/sec), was estimated by the formula

$$Q_w = V.L.D.$$

where V = mean vertical velocity of rising water in 50–100 m layer (cm/sec);
L = extension of the rising water zone on the section (cm);
and D = width of rising water zone on the section (= 1 cm).

The gradient-convectional component of vertical velocity was calculated by the method of K. Hidaka (Tjuryakov, 1965).

The mean values of horizontal and vertical water transport in March to May were calculated for the period 1962–74, excluding 1965 and 1966 when observations were not carried out.

The mean catch (in numbers) of 2-year-old cod per trawling hour was taken as the relative index of recruitment to the Flemish Cap cod stock (Table 1).

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[1] Submitted to the June 1978 Annual Meeting as ICNAF Res. Doc. 78/VI/23.

TABLE 1. Average catch of 2-year-old cod per hour trawling from survery on the Flemish Cap in 1962-74. (From Konstantinov and Noskov, MS 1978.)

Year-class of cod	Number per hour trawling
1962	7
1963	6
1964	1
1967	13
1968	106
1969	2
1970	1
1971	87
1972	29
1973	350
1974	50

Results

Analyses of the available data indicate the frequent occurrence of cyclonic eddies on the southern and eastern slopes of the Flemish Cap whereas a quasi-steady clockwise water circulation exists on the central part of the bank. Statistical analysis of the horizontal parameters of this anticyclonic circulation indicated insignificant misalignment of its axis from the central part of the bank at about 47°09'N, 45°21'W, whereas the cyclonic eddy areas may vary within rather broad limits.

Figures 1 to 3 show the distribution by depth of the velocity of the horizontal geostrophic current and the vertical water movements, as well as the distribution of phosphates and dissolved oxygen, on the 47°N section between 46°29'W and 44°05'W in May of 1970, 1972 and 1973. These diagrams clearly demonstate the relationship between the vertical water movement and the degree of anticyclonic eddy development, as well as the relationship between the distribution of phosphates and dissolved oxygen and the zones of vertical water movement. Judgement about the development of phytoplankton in an area can be made on the basis of the phosphate content of the surface layer, as zones rich in nutrient salts usually correspond to areas of maximum development of phytoplankton (Maximova, 1976). Hence the intensity of the horizontal and vertical water circulation over the central part of Flemish Cap during the period of development of cod eggs and larvae is one of the main abiotic factors regulating year-class abundance.

Using the relative abundance indices (N) for 2-year-old cod (Table 1), the relationship between year-class strength and the parameters defining the horizontal and vertical water circulation was determined by multiple correlation analysis to be

$$N = 0.20\,Q_s + 0.36\,Q_w - 175.38$$

where Q_s = total horizontal water transport per time unit (10^{-3} m^3/sec) in the 0-100 m layer across the 47°N section based on 6 stations between 46°29'W and 44°05'W;

and Q_w = volume of water rising per time unit (cm^3/sec) in the 50-100 m layer on the 47°N section.

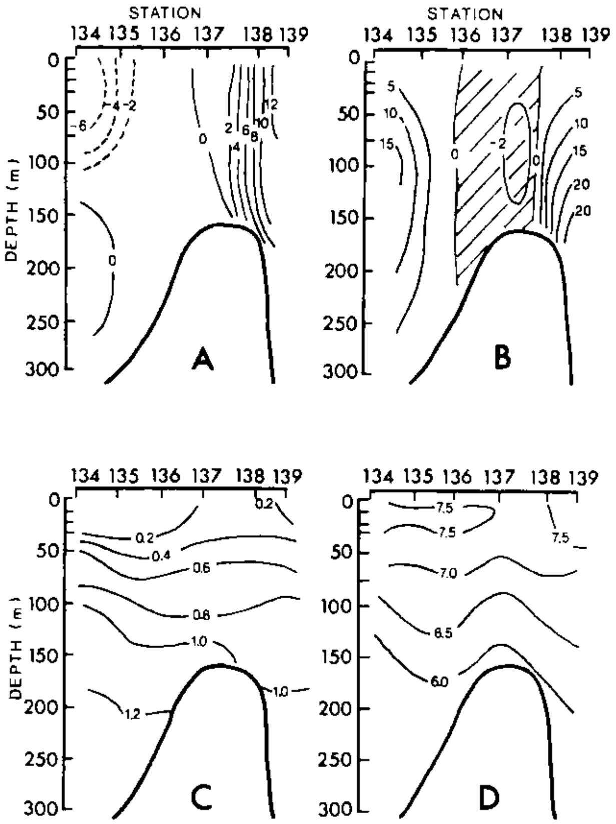

Fig. 1. Water characteristics on section 6A across Flemish Cap in May 1970. A. Geostrophic horizontal velocity, V cm/sec (minus to the north and plus to the south). B. Vertical velocity, W cm/sec × 10^5 (minus for rising and plus for lowering water). C. Phosphates. P µg atoms/l. D. Dissolved oxygen. O_2 ml/l

The coefficient of multiple correlation was calculated to be 0.867, indicating that the most abundant year-classes of cod appear during years of intensive water movements (well-defined anticyclonic eddy and strong upwelling) over the central part of the bank during the development period of cod eggs and larvae in March to May. This method, therefore, seems to be useful as a means of forecasting year-class strength of cod on the Flemish Cap well in advance of their recruitment to the commercial fishery.

Conclusions

1. There is a quasi-steady circulation of anticyclonic water motion over the central part of the Flemish Cap.

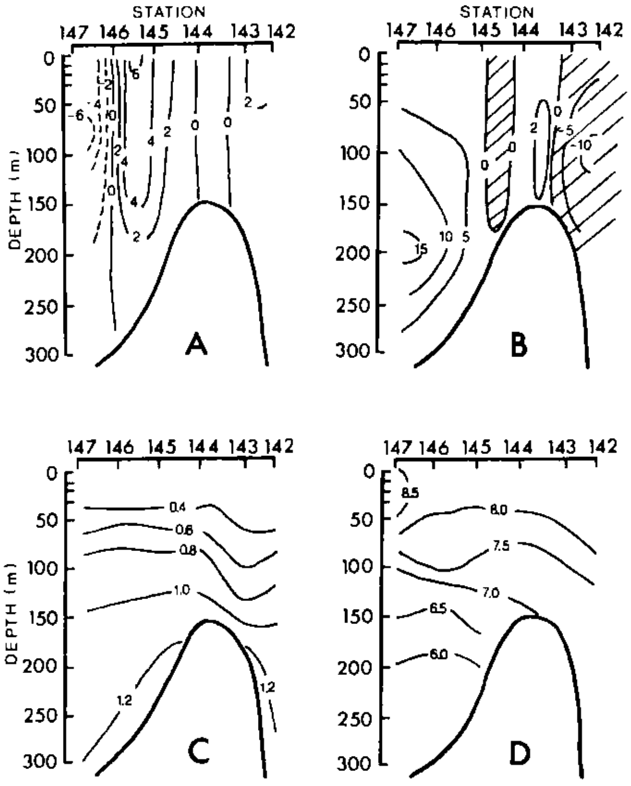

Fig. 2. Water characteristics on section 6A across Flemish Cap in May 1972. (See Fig. 1 legend for key to diagrams.)

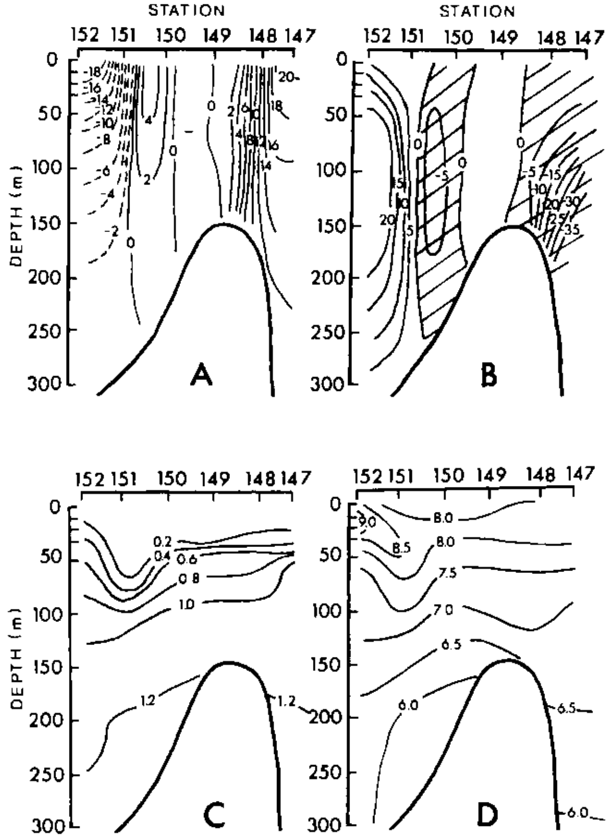

Fig. 3. Water characteristics on section 6A across Flemish Cap in May 1973. (See Fig. 1 legend for key to diagrams.)

2. One of the main abiotic environmental factors regulating the abundance of cod year-classes on the Flemish Cap is the intensity of the horizontal and vertical water circulation over the central part of the bank during the development period of cod eggs and larvae.

3. It is suggested that parameters defining the water circulation over the Flemish Cap can be used to assess the relative strength of cod year-classes well in advance of their recruitment to the commercial fishery.

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Back-Calculation of Length-At-Age from Otoliths for Silver Hake of the Scotian Shelf[1]

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Abstract

Measurement of silver hake otoliths indicates a linear relationship between both half and total otolith length and fish length. Back-calculated lengths and derived mean lengths-at-age were used to construct von Bertalanffy curves, which appear to adequately describe the growth of silver hake over the first 5 years, and these are comparable with other estimates of growth.

Introduction

Age and growth of silver hake, *Merluccius bilinearis*, have been a subject of study by international researchers and have been discussed at several ageing workshops (ICNAF, MS 1976, MS 1977, MS 1978). While progress has been made in attempts to resolve differing interpretation of otoliths, variation in juvenile growth rates, both within stocks and between stocks, has continued to cause problems in estimating age. To date, age validation studies have consisted of comparison of otolith-derived ages with age compositions generated from length frequency analysis (Hunt, 1978). Results of these studies have provided mean lengths-at-age and growth curves for silver hake which appear to adequately describe growth characteristics of this species on the Scotian Shelf (ICNAF Div. 4VWX).

Back-calculation of length-at-age from otoliths, scales or other indicators of growth may also be considered a method of age validation subject to at least two limitations: some otolith dimension must be related to size of the fish, and the zones measured must be related to a time scale. This study attempts to measure growth zones in silver hake otoliths and to relate these measurements to fish age at the time of zone formation.

Material and Methods

An international sampling program with Canadian observers on board of foreign fishing vessels was initiated by Canada in 1977. Observers sampled silver hake catches of Cuba, Japan and USSR from April to September for length frequency distribution and collected otoliths on a length-stratified basis. The otoliths were stored dry in envelopes with individual length and sex data and were available from most regions of commercial fishing on the Scotian Shelf. Samples were selected at random by month (87 samples, 2,143 fish) from those available, for age determination and 30 of these samples were chosen by month and area for otolith measurement. These 30 samples consisted of 689 otoliths collected from April to September, of which 82 otoliths were discarded because of fragmentation. Date, location and number of fish sampled are summarized in Table 1 where location refers to the lower right corner of the 10' x 10' rectangle in which the fish were caught. The samples, consisting mostly of 20–30 fish each, were collected in an area bounded by 42°40' and 44°00'N latitude and 60°10' and 64°30'W longitude.

The right and left otoliths were assumed to be equivalent except in abnormal cases, and whichever of the two was more complete (i.e. unbroken) was selected for examination. Dry otoliths were found to be opaque and unreadable, but, through trial and error, it was found that immersion in a saturated saline solution for a minimum of 24 hours cleared the otolith sufficiently for examination. Otoliths prepared in this was were examined in alcohol by reflected light at a magnification of 12x using a stereo microscope with a black background. Several techniques for measuring otoliths were considered and the most efficient was found to be the use of a camera lucida attachment. A scale with fine increments was superimposed on the otolith through the camera lucida and the incident light on the otolith and scale matched for optimum viewing. Orientation of the scale on the otolith was facilitated since movement of the scale relative to the otolith was reduced by the magnification factor. This system provided a total magnification of 15x and one eye piece unit (EPU) was equal to 0.03387 mm with a resultant accuracy of about 0.02 mm.

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[1] Submitted to the June 1978 Annual Meeting as ICNAF Res. Doc. 78/VI/42.

TABLE 1. Numbers of silver hake sampled for otolith measurements by month and location on Scotian Shelf, 1977. (Position refers to lower right corner of 10' X 10' rectangle where sample was taken.)

Month	Location		No. of Fish	No. of Otoliths
	Latitude	Longitude		
Apr	42°50'	62°50'	17	13
	43°20'	60°40'	26	25
	43°10'	63°50'	25	23
	42°40'	63°40'	31	22
	Total		99	83
May	43°20'	60°40'	25	25
	42°50'	61°50'	33	29
	42°50'	62°40'	27	24
	42°40'	63°50'	36	33
	43°50'	63°40'	33	26
	Total		154	137
Jun	42°50'	62°20'	15	14
	42°50'	62°00'	22	21
	42°50'	62°20'	21	8
	43°20'	60°30'	21	21
	42°50'	62°00'	20	17
	42°50'	62°20'	24	18
	42°50'	62°10'	17	15
	42°30'	64°30'	20	19
	42°40'	64°10'	29	22
	Total		189	155
Jul	44°00'	58°30'	15	15
	43°10'	61°20'	25	25
	43°20'	60°30'	25	24
	43°50'	60°10'	22	20
	43°00'	61°20'	21	21
	Total		108	105
Aug	44°00'	58°30'	21	19
	43°30'	63°00'	32	29
	42°50'	63°00'	8	8
	43°20'	60°40'	18	17
	43°30'	63°00'	17	16
	Total		96	89
Sep	43°00'	62°00'	25	22
	42°50'	61°00'	18	16
	Total		43	38
	Grand total		689	607

Measurements of each otolith consisted of the total length (TL), when possible, the half length (HL) and the distance from the center of the nucleus to the middle of each hyaline zone (O_1, O_2, ...O_n). Definition of these measurements is shown in Fig. 1.

Regressions of otolith dimension and fish length of the form Y = A + BX were completed to establish if a linear relationship existed between the respective measurements. The relationship between total and half otolith lengths was also examined. The lengths at which respective hyaline zones were formed could then be calculated using direct proportionality.

Lengths determined in this way were not related to time, but it was assumed that lengths corresponding to the annuli would represent the lengths at 1 January, since measurement was made to the center of the hyaline zone which forms from late autumn to early spring. Also, a frequency distribution of calculated lengths should indicate concentrations related to age groups, and lengths obviously outside of these concentrations might then be attributed to checks or false annuli. Comparison of mean lengths derived from these measurements with those for fish which had been aged or for which mean lengths-at-age had been derived using other techniques would allow assessment of age validity.

Results

A total of 195 otoliths were measured for total length (TL in EPU) and a graph of these lengths against fish length (FL in cm) is shown in Fig. 2. Visual inspection of the scatter diagram suggested a linear relationship, and the line

$$FL = 1.85 + 0.07\ TL$$

was found to be the best fit with a resultant regression coefficient (R^2) of 0.89 for fish in the length range of 15–45 cm, which includes the size of most fish in the silver hake fishery. The mean fish length was 28.3 cm and the mean otolith length was 386.6 EPU.

The scatter diagram (Fig. 3) of fish length (cm) and otolith half length (EPU) also suggests a linear relationship, and the line

$$FL = 0.59 + 0.17\ HL$$

was found to give the best fit with R^2 of 0.83, based on a sample size of 588 fish. Mean fish and otolith lengths were 30.5 cm and 175.5 EPU respectively. This linear relationship established a direct proportionality between fish length and otolith length and allowed use of the equation:

$$FL_n = FL_t \times O_n / O_{HL}$$

from which the fish length at which zones were formed could be calculated. As a further check of consistent measurements, the relation between total and half otolith length was found to be linear ($HL = 14.4 + 0.39\ TL$, $R^2 = 0.92$) and Fig. 4 shows this relationship.

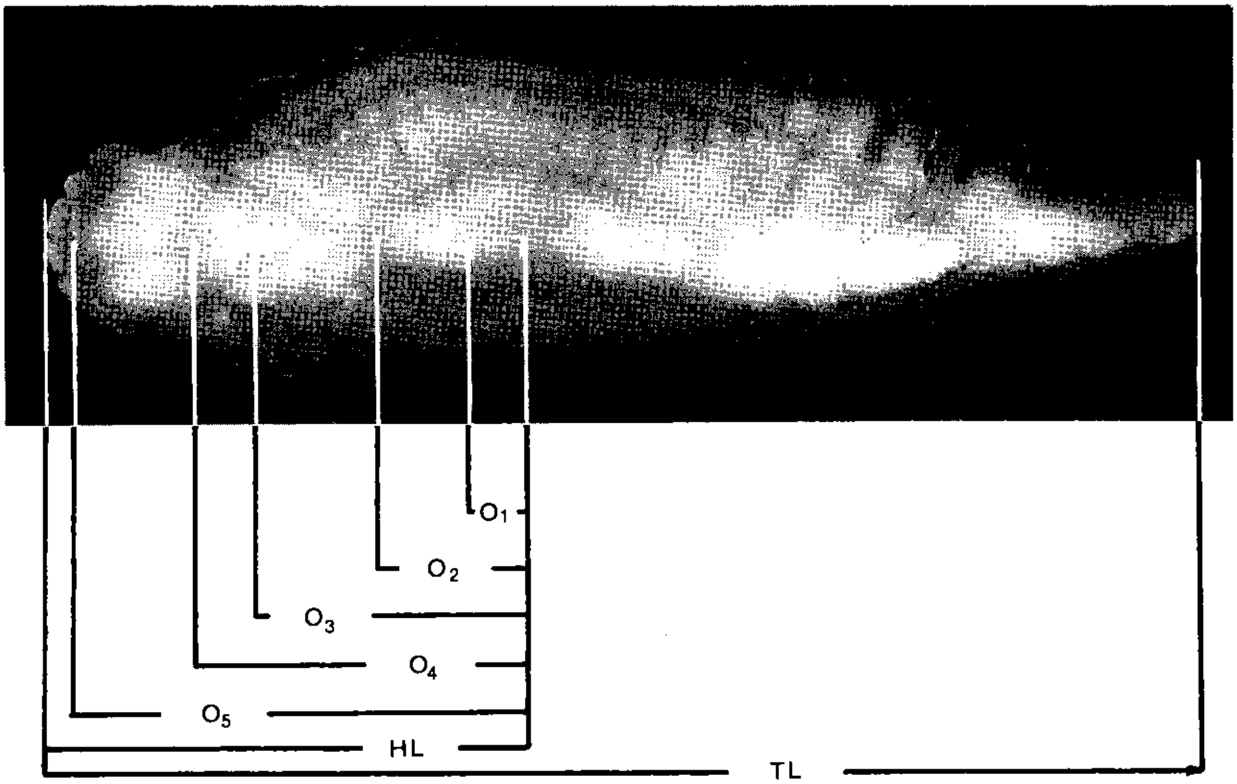

Fig. 1. Photographs of a silver hake otolith with key to measurements.

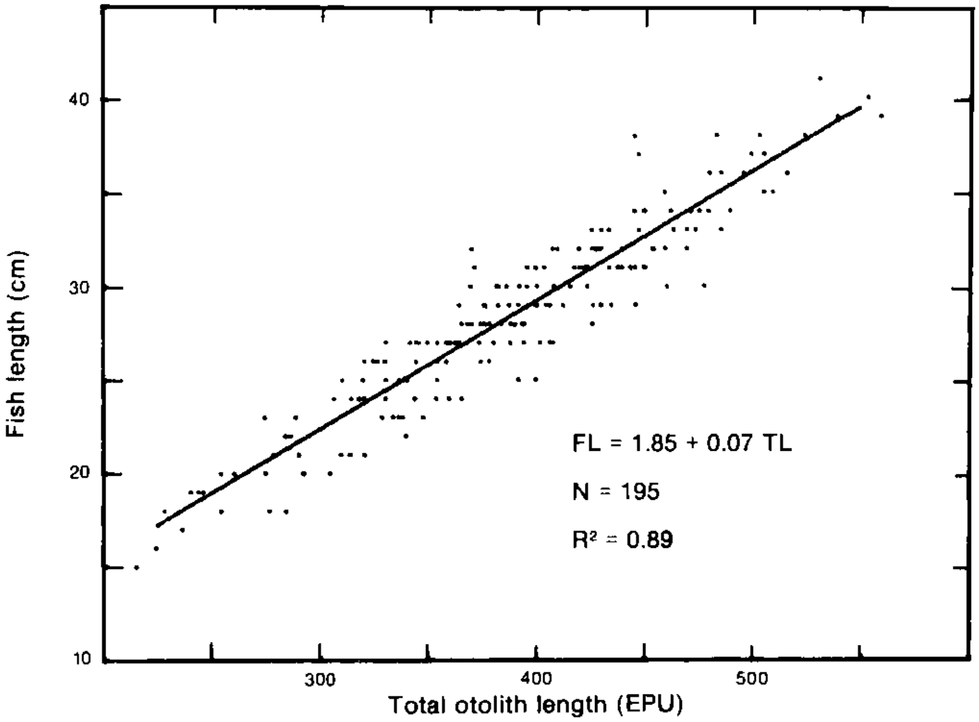

Fig. 2. Regression of total otolith length (TL) on fish length (FL) for silver hake from Scotian Shelf.

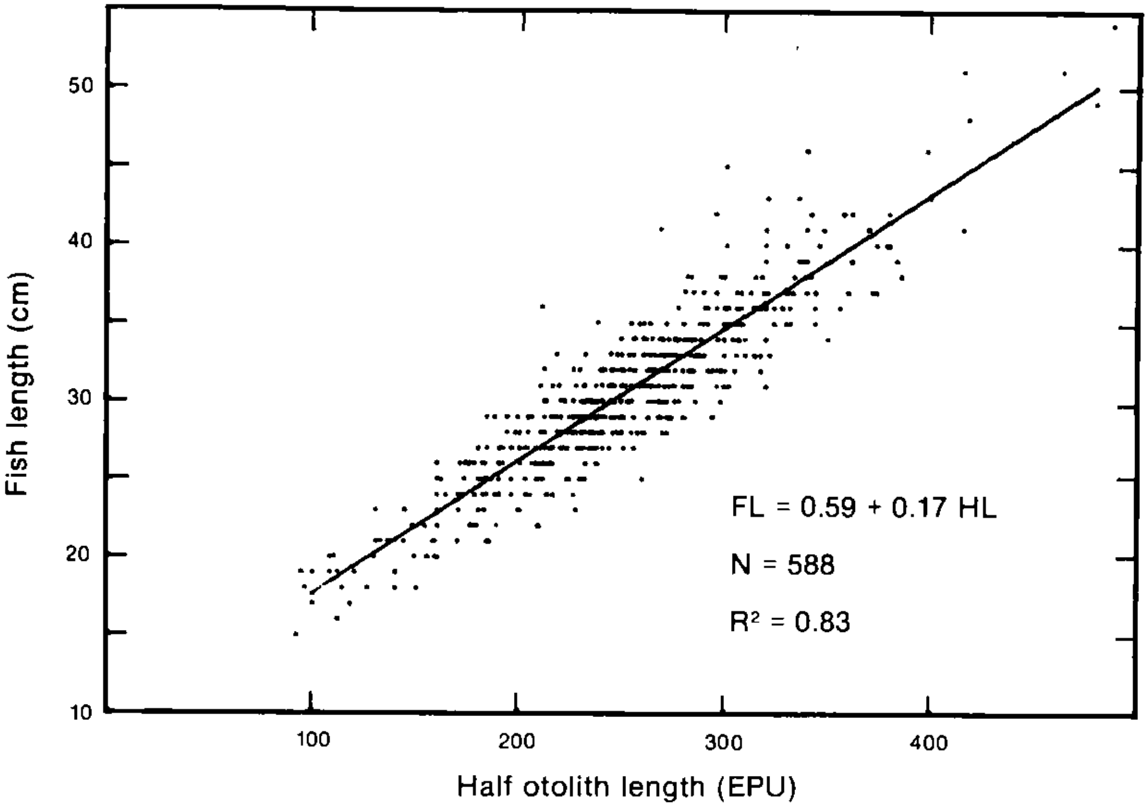

Fig. 3. Regression of half otolith length (HL) on fish length (FL) for silver hake from Scotian Shelf.

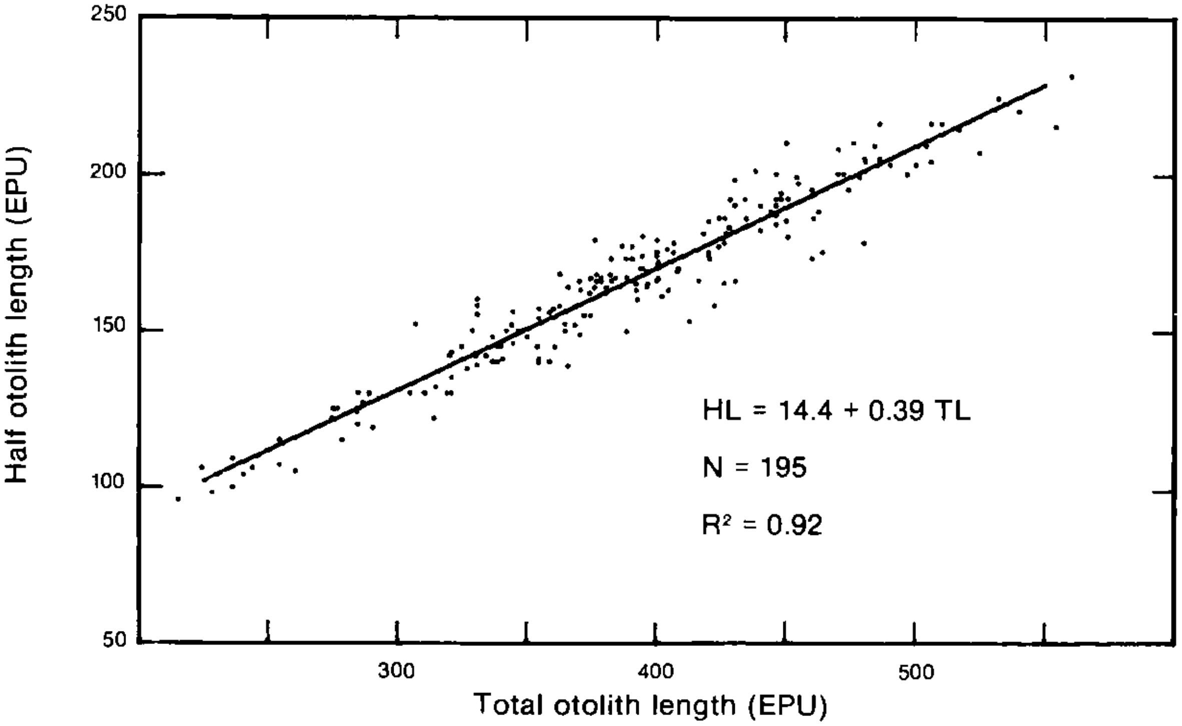

Fig. 4. Regression of total otolith length (TL) on half otolith length (HL) for silver hake from Scotian Shelf.

TABLE 2. Back-calculated lengths of silver hake by age group. (P = pelagic zone; C = check; Mean lengths in mm.)

	Male									Female									Combined								
Length (cm)	P	1	C	2	C	3	C	4	Total	P	1	C	2	C	3	C	4	Total	P	1	C	2	C	3	C	4	Total
3										1								1	1								1
4	3								3	2								2	5								5
5	2								2	2								2	4								4
6	4	1							5	7								7	11	1							12
7	8	—							8	6								6	15	1							16
8	2	5							7	8	6							14	10	11							21
9	5	11							16	1	12							13	7	23							30
10	1	19							20	2	16							18	3	35							38
11	1	25							26	1	31							32	2	56							58
12		35							35		23							23		58							58
13		35							35		29							29		66		1					67
14		22							22		30							30		53		—					53
15		17							17		25							25		42		—					42
16		19	1	1					21		15							15		34	1	1					36
17		11	1	3					15		13		2					15		24	1	5					30
18		4	—	5					9		8	1	3					12		12	1	8					21
19		7	1	11					19		8	—	7					15		15	1	18					34
20		5	—	14					19		6	—	10					16		11	—	24					35
21		—	—	25					25		3	4	16					23		3	4	41					48
22		—	—	27	1				28		5	—	20		1			26		5	—	47	1	1			54
23		2	3	31	—	1			37		1	1	38		—			40		3	4	69	—	1			77
24		2	2	34	—	3			41		—	—	38		1			39		2	2	72	—	4			80
25		1	4	36	—	6			47		2	1	35	2	3			43		3	5	71	2	9			90
26		1	4	27	4	12		1	49		2		50	4	2			58		3	4	77	8	14		1	107
27			2	20	4	18		—	44		1		37	4	10			52		1	2	57	8	28		—	96
28				13	3	16		—	32				14	4	25			43				27	7	41		—	75
29				5	1	22	1	3	32				14	6	29		1	50				19	7	51	1	4	82
30				2	—	30	—	3	35				7	5	26	1	3	42				9	5	56	1	6	77
31				1	—	16	1	2	20				4	1	38	—	6	49				5	1	54	1	8	69
32					1	7	1	2	11				2	3	32	1	13	51				2	4	39	2	15	62
33						2		7	9				1	—	20	2	10	33				1	—	22	2	17	42
34						1		1	2					1	6	—	18	25					1	7	—	19	27
35						1		2	3					1	16	1	15	33					1	17	1	17	36
36								—	—						6	—	14	20						6	—	14	20
37								1	1						3	1	5	9						3	1	6	10
38															2		3	5						2		3	5
39															—		5	5						—		5	5
40															—		5	5						—		5	5
41															1		4	5						1		4	5
42																	—	—								—	—
43																	1	1								1	1
44																	—	—								—	—
45																	1	1								1	1
Total No.	26	222	18	255	14	135	3	22	695	30	236	7	298	31	221	6	104	933	58	462	25	554	45	356	9	126	1,635
Mean L (mm)	76	140	242	242	276	293	312	324	216	75	145	219	253	293	314	338	355	247	76	142	236	248	288	306	329	349	235

A frequency distribution of the back-calculated lengths-at-age is presented in Table 2 and summarized in Fig. 5. Of the 1,642 measurements taken, 692 were for males, 944 for females and 6 for unsexed fish. These distributions for males and females (Fig. 5) do not suggest significant variation between months but they appear to consist of several modes. Visual inspection indicates a distinct break in frequency at about 20 cm with fish above and below this length divided into two or more groups. Also, the maximum size for females tended to be greater than that for males, suggesting larger mean lengths-at-age for females at least for the older fish.

Otoliths had been aged prior to measurement and it was possible to assign ages to zones based on the estimated overall age of the fish. Prior research (Hunt, 1978) suggested the presence of a pelagic zone as well as frequent checks between annuli, and zones were identified with respect to these criteria to yield a series of back-calculated lengths for each otolith corresponding to ages 1, 2, 3 and 4 as well as to the pelagic zone (P) and intermediate checks (C). The results are summarized by sex in Table 3 and include estimated mean fish lengths for the various hayline zones. The back-calculated lengths of age 1 males and females have a wide range which suggests incorrect ageing, sampling error or combination of fast- and slow-growing individuals. Of these, incorrect ageing seems more probable, implying, for example, that a fish aged as 3 years was actually 4, or that a zone identified as age 1 should have been 2, or that a pelagic zone, if present, should have been called age 1, etc. It is possible that the pelagic zone has been confused with the first annulus, but this is probably limited to less than 5% of the total.

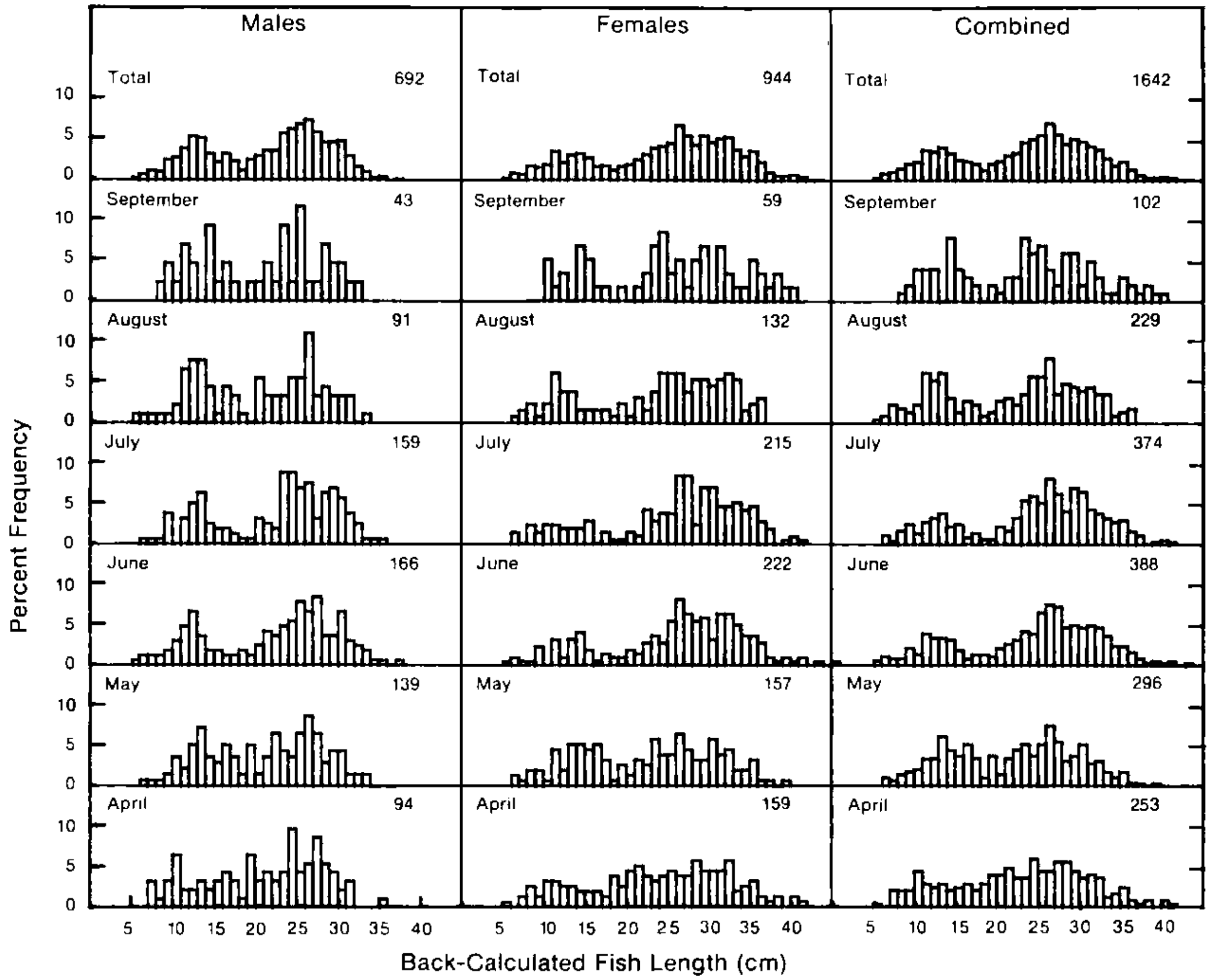

Fig. 5. Frequency distributions of back-calculated lengths for silver hake from Scotian Shelf. (The number of specimens examined is given for each distribution.)

TABLE 3. Means lengths-at-age and otolith dimensions for silver hake on Scotian Shelf, derived from back-calculated lengths assuming 1 January as the birthdate. (SD = standard deviation; Range = ± 3 SD.)

		Fish length (cm)			Otolith dimension (mm)		
Sex	Age (yr)	Mean	SD	Range	Mean	SD	Range
Male	0.5	14.0	3.29	4.1-23.9	3.22	1.44	1.58-4.85
	1.5	24.2	2.81	15.8-32.6	4.91	1.36	3.51-6.31
	2.5	29.3	2.19	22.7-35.9	5.76	1.26	4.67-6.85
	3.5	32.4	2.44	25.1-39.7	6.27	1.30	5.06-7.49
Female	0.5	14.5	3.66	3.5-25.5	3.30	1.50	1.48-5.12
	1.5	25.3	2.85	16.8-33.9	5.09	1.37	3.67-6.51
	2.5	31.4	2.77	23.1-39.7	6.10	1.35	4.73-7.48
	3.5	35.5	3.03	26.4-44.6	6.78	1.40	5.28-8.29
Combined	0.5	14.2	3.50	3.7-24.7	3.25	1.47	1.51-4.99
	1.5	24.8	2.92	16.0-33.6	5.01	1.38	3.56-6.46
	2.5	30.6	2.77	22.3-38.9	5.97	1.35	4.59-7.35
	3.5	34.9	3.17	25.4-44.4	6.69	1.42	5.11-8.26

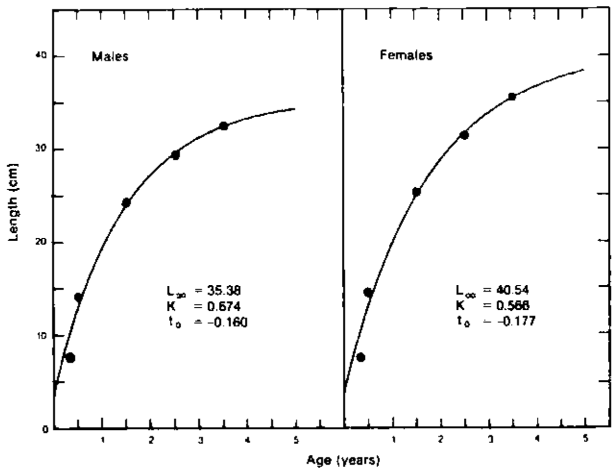

Fig. 6. Von Bertalanffy growth curves derived from back-calculated mean length-at-age for silver hake from Scotian Shelf.

Von Bertalanffy curves were fitted to the back-calculated length-at-age for males and females, assuming that the age at formation of the first annulus was 0.5 year based on a 1 January date and a July spawning period. Other annuli were equated to 1.5, 2.5 and 3.5 years. The parameters of the growth curves are as follows:

	K	L_∞	t_0
Males	0.674	35.38	-0.160
Females	0.566	40.54	-0.177

Curves illustrating these growth patterns are shown in Fig. 6 and indicate a good fit to the data with apparent differences between the sexes.

Otolith dimensions calculated from the mean and standard deviation of length-at-age are shown in Table 3. The estimated size of the pelagic zone is probably larger than the true value since the zone is generally obscured in larger fish and may not appear as a distinct hyaline zone when small in size.

Conclusions

Analysis of otolith dimensions relative to fish length suggest that a linear relationship exists between both the total and half otolith lengths and fish length of silver hake. This proportionality allows the back-calculation of length-at-age from otoliths from which frequency distributions can be generated. These distributions should consist of components corresponding to some physiological event in the life of the fish which may be reflected in the otolith by formation of a hyaline zone. For the most part, these zones may be assumed to indicate winter growth and may thus be equated to annuli and the length associated with a zone related to time or age in years.

The results indicate that an age-length key derived from back-calculated lengths is consistent with those based on total age with adjustment for time of year. Growth rates of male and female silver hake appear to diverge above 25 cm and females reach a larger asymptotic length. Von Bertalanffy growth curves appear to adequately describe growth of males and females in the initial 5 years, and the parameters of these curves are comparable with those derived from total age.

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Estimating the Accuracy of Abundance Indices for Silver Hake from Surveys in the Emerald Deep Area of the Scotian Shelf, 1972-76[1]

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Abstract

The accuracy of abundance indices for silver hake from trawling surveys of the Emerald Deep area (ICNAF Div. 4W) in 1972-76 was estimated by studying the statistical characteristics of the catch per haul, by comparison with other independent stock size estimates, and by the method of statistical simulation. The accuracy of the abundance index is considered to be relatively low, varying about ±20% from the mean, and rather large discrepancies are noted between stock size estimates derived from time series of USSR and Canadian survey data and from virtual population analysis. The frequency distribution of catches appear to conform to a negative binomial distribution, the application of which may be useful in analyzing the accuracy of abundance indices. Computer simulations indicate that increasing the number of hauls for the survey is not an efficient method of improving the accuracy.

Introduction

USSR research vessels have conducted annual trawling surveys in the Emerald Deep area of the Scotian Shelf during 1972-76, primarily to study the distribution, abundance and biological characteristics of silver hake. According to Noskov (MS 1976) and Doubleday *et al.* (MS 1976), about 90% of the commercial catch of silver hake on the Scotian Shelf is taken in and near the Emerald Deep area. Therefore, the estimation of abundance indices derived from survey data from this area is of great interest in assessing the silver hake stock.

The whole of the Emerald Deep area was treated as a single stratum, in which 20 hauls were made annually in the autumn at randomly selected locations. The mean catch per standard haul (30 min duration) both in numbers and weight was used as an abundance index.

Two approaches to the estimation of the accuracy of abundance indices from trawling surveys are widely used, as discussed by Grosslein (1971). One approach is to study the statistical characteristics of the catch-per-haul data derived from stratified-random sampling surveys, and the other is based on correlating survey abundance indices with other independent sets of data, such as biomass estimates from virtual population analysis. Both approaches suffer from short-comings. In the first case, the sampling variance is used as an indicator of the precision of the abundance index derived from a set of survey data, but this parameter does not necessarily imply a high degree of precision if the frequency distribution of catches deviate significantly from a normal distribution. In the second case, the validity of a time series of abundance indices based on research vessel surveys requires that these data be correlated with one or more independent sets of observations derived from other sources, e. g. the commericial fishery.

Apart from the approaches mentioned above, a method of computer simulation is suggested to examine the accuracy of trawling survey data. This method, based on probability theory, involves the analysis of irregularities in the spatial distribution of catches which may provide supplementary information on the accuracy of the abundance index.

Accuracy of the Abundance Index from its Statistical Characteristics

The mean catch per haul in a given stratum and its variance are calculated from the standard formulae:

$$\bar{x} = \frac{1}{n} \sum_{i=1}^{n} x_i$$

and

$$s_{\bar{x}}^2 = \frac{1}{n(n-1)} \sum_{i=1}^{n} (x_i - \bar{x})^2$$

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where $\bar{x}$ = mean catch per haul in a stratum,
$s_{\bar{x}}^2$ = variance of the mean catch per haul,
x_i = catch in the *i*th haul, and
n = number of hauls in the stratum.

The results of the calculations for silver hake catches in surveys of the Emerald Deep area in 1972-76, in terms of the actual catches by number and by weight are given in Table 1. Since frequency distributions of catches tend to be skewed, a logarithmic transformation was applied in order to normalize the data, and the results of these calculations are shown in Table 2. On the average, the coefficient of variation of the abundance index is 20% for the untransformed data and 5% for the transformed data. Although the mean catch per haul varied by a factor of 3 during the period, the rather wide ranges of the 95% confidence intervals suggest that year-to-year variation in the silver hake stock was not distinguishable from sampling fluctuations.

For comparison with the silver hake survey data, the coefficients of variation, derived by Grosslein (1971) for cod, haddock and yellowtail flounder on Georges Bank, averaged 25% (16-43%) for the actual catch per haul data (by weight) and 13% (5-18%) for the transformed (natural logarithm) data. These values are higher than those for silver hake survey data from the Emerald Deep area.

Comparison with Other Abundance Indices

The silver hake abundance indices from USSR surveys in 1972-76 are compared in Fig. 1 with estimates of stock size in Div. 4VWX derived from virtual population analysis (Noskov, MS 1976) and with abundance indices from Canadian surveys in Div. 4VWX (Doubleday, Hunt, and Halliday, MS 1976). The indices are plotted in terms of the percentage deviation from the mean for each set of data illustrated. The USSR survey abundance index was highest in 1975 when the virtual population analysis estimate of stock size was lowest, and the Canadian survey abundance index was relatively high in 1973 and 1974 when the biomass was declining. It is obvious from Fig. 1 that the data are not well correlated, but one would hardly consider the presence or absence of a correlation from such a short time series of observations. Such

TABLE 1. Mean catch per hour in numbers (A) and by weight in kg (B), and associated estimates of precision, for silver hake from trawling surveys in the Emerald Deep area, 1972-76.

	Year	Catch per haul $\bar{x}$	Variance s^2	Standard deviation s	$\frac{s}{\bar{x}}$	Confidence interval $\bar{x}-2s$	$\bar{x}+2s$
A.	1972	963	43,681	209	0.22	545	1,381
	1973	866	34,225	185	0.21	496	1,236
	1974	1,291	38,025	195	0.15	901	1,681
	1975	2,635	311,364	558	0.21	1,519	3,751
	1976	1,508	108,900	330	0.22	848	2,168
B.	1972	101	361	19	0.19	63	139
	1973	116	484	22	0.19	72	160
	1974	205	1,089	33	0.16	139	271
	1975	340	4,761	69	0.20	202	478
	1976	227	2,704	52	0.23	123	331

TABLE 2. Mean catch per hour (natural logarithm transformation) in numbers (A) and by weight in kg (B), and associated estimates of precision, for silver hake from trawling surveys in the Emerald Deep area, 1972-76.

	Year	*ln* (catch per haul) $\bar{x}$	Variance s^2	Standard deviation s	$\frac{s}{\bar{x}}$	Confidence interval $\bar{x}-2s$	$\bar{x}+2s$
A.	1972	6.25	0.0784	0.28	0.04	5.69	6.81
	1973	6.31	0.0576	0.24	0.04	5.83	6.79
	1974	6.84	0.0484	0.22	0.03	6.40	7.28
	1975	7.44	0.0529	0.23	0.03	6.98	7.90
	1976	6.79	0.0625	0.25	0.04	6.29	7.29
B.	1972	4.10	0.0784	0.28	0.07	3.54	4.66
	1973	4.40	0.0441	0.21	0.05	3.98	4.82
	1974	4.97	0.0529	0.23	0.05	4.51	5.43
	1975	5.40	0.0529	0.23	0.04	4.94	5.86
	1976	4.91	0.0576	0.24	0.05	4.43	5.39

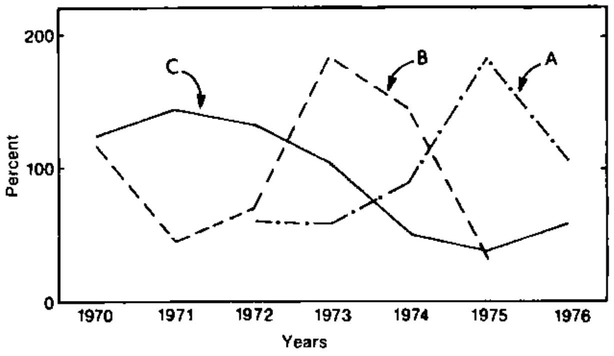

Fig. 1. Comparison of abundance indices for silver hake on the Scotian Shelf based on (A) USSR surveys in the Emerald Deep area, (B) Canadian surveys in Div. 4VWX (Doubleday, Hunt and Halliday, MS 1976), and (C) virtual population analysis of Div. 4VWX stock (according to Noskov, MS 1976).

instances of inconsistency between abundance indices from different sources are not uncommon. For example, Grosslein (1971), in his analysis of research and commercial abundance indices for cod, haddock and yellowtail in 1963-69, indicated similar inconsistences for cod on Georges Bank (Div. 5Z) and haddock off southwest Nova Scotia (Div. 4X).

Regularities in the Spatial Distribution of Silver Hake

Taylor (1953) concluded, from his analysis of variability in survey trawl catches on Georges Bank in 1948-50, that the frequency distribution of catch-per-haul data approximates the negative binominal distribution. Such a distribution may be derived from different models. However, the most common biological interpretation is to assume that the spatial distribution of individuals clustered in groups is random (Poisson distribution) and that the number of individuals in a group fits the logarithmic series distribution.

The probability of occurrence of r individuals is determined by the formula:

$$P(r) = \frac{\Gamma(r-k)p^r}{r!\,\Gamma(k)q^{k-r}}$$

where Γ represents a gamma function, $p = m/k$, $q = 1 - p$, m is mean of the observed distribution, and k is a parameter relating the variance (d^2) of the distribution with the mean, such that $d^2 = m + m^2/k$.

In view of the limited number of observations for silver hake in the Emerald Deep area, the hypothesis that the distribution of catches conforms with the negative binomial distribution was first checked by using data from comparative gear experiments during the joint USSR-USA surveys for groundfish in 1973-75. The results, using χ^2 as the "goodness of fit" criterion for four sets of data (Table 3), verify the hypothesis that the distribution of catches conform to the negative binomial distribution.

A direct check of the hypothesis that the survey data for silver hake from the Emerald Deep area

TABLE 3. Observed and expected (based on fitting the negative binomial distribution) catches of silver hake in USSR-USA comparative gear experiments: (A) No. 41 Yankee trawl, 1973; (B) No. 36 Yankee trawl, 1973; (C) No. 41 Yankee trawl, 1974; (D) No. 36 Yankee trawl, 1974; (E) No. 41 Yankee trawl, 1975; (F) No. 36 Yankee trawl, 1975.

	Catch/haul (numbers)	Number of hauls		χ^2
		Observed	Expected	
A.	0-15	40	49	1.68
	16-50	13	9	1.65
	51-100	8	5	0.73
	101-200	8	6	0.49
	201-500	11	8	0.98
	501-1000	4	5	0.30
	1001-2000	1	3	1.80
	2001-5000	3	1	0.95
	Total	88	86	8.58
B.	0-15	53	61	1.11
	16-50	21	11	7.60
	51-100	9	6	0.78
	101-200	2	5	2.47
	201-500	4	4	0.07
	501-1000	1	1	0.01
	Total	90	88	12.04
C.	0-15	41	38	0.12
	16-50	6	13	3.98
	51-100	9	8	0.003
	101-200	12	9	0.80
	201-500	10	9	0.001
	501-1000	4	3	0.006
	1001-2000	1	1	0.005
	Total	83	81	4.91
D.	0-15	45	41	0.36
	16-50	13	17	1.20
	51-100	11	11	0.002
	101-500	17	16	0.04
	501-1000	1	0	0.005
	Total	87	85	1.61
E.	0-15	20	39	9.36
	16-50	45	24	16.92
	51-100	16	17	0.11
	101-200	15	16	0.08
	201-1000	12	13	0.21
	Total	108	109	26.68
F.	0-15	80	82	0.05
	16-50	19	16	0.41
	51-100	6	8	0.72
	101-200	5	5	0.15
	201-1000	3	3	0.01
	Total	113	114	1.34

conforms with the negative binomial distribution was made using the method of moments (Anscombe, 1950; Bliss, 1953) based on consideration of the difference (T) between the third moments obtained theoretically and empirically, where

$$T = \frac{x^3}{n} - d^2\left\{\frac{d^2}{m} - 1\right\}$$

where $\left\{\frac{x^3}{n}\right\}$ is the third moment and d^2 and m are the variance and mean of the negative binomial distribution. The variance of T was determined from the formula

$$Var(T) = 2m\ (k+1)\ p^2\ q^2\ n^{-1}\ [2(3+5p) + 3kq]$$

The results of the computations (Table 4) indicate that the distribution of silver hake catches from surveys in the Emerald Deep area is consisent with the hypothesis of a negative binomial distribution. It should be noted that this hypothesis also fits the data on stratum mean catch and variance presented by Hennemuth (MS 1976), giving further evidence of its usefulness in analyzing survey data.

Accuracy of Abundance Indices Using Simulation Methods

The method of statistical simulation for estimating the accuracy of trawl survey data is one of the promising approaches which may be applied in the absence of a *priori* information. The method requires making an assumption about the type of probability distribution to which the spatial distribution of the population is expected to conform. With appropriate probability characteristics of catch as a random variable for a given number of hauls, the statistical characteristics of the precision of the method may be simulated, the lack of a *priori* information being compensated with repetitive calculations using the parameters of the hypothesized distribution and the possible range of their variation.

The parameters of the negative binomial distribution derived from trawl survey data for silver hake in the Emerald Deep area during 1972-76 were used in the simulations. As indicated in Table 4, the mean catch per haul varied from 850 to 2,600 individuals and the coefficient k ranged from about 1.0 to 2.3. The simulations were therefore made using m = 500, 1,500 and 2,500, and k = 0.5, 1.25 and 2.0; 20 hauls were taken as the number generally accepted in practice.

The results of the experiments based on 500 computer runs of the model are presented as histograms in Fig. 2-4. Some conculsions resulting

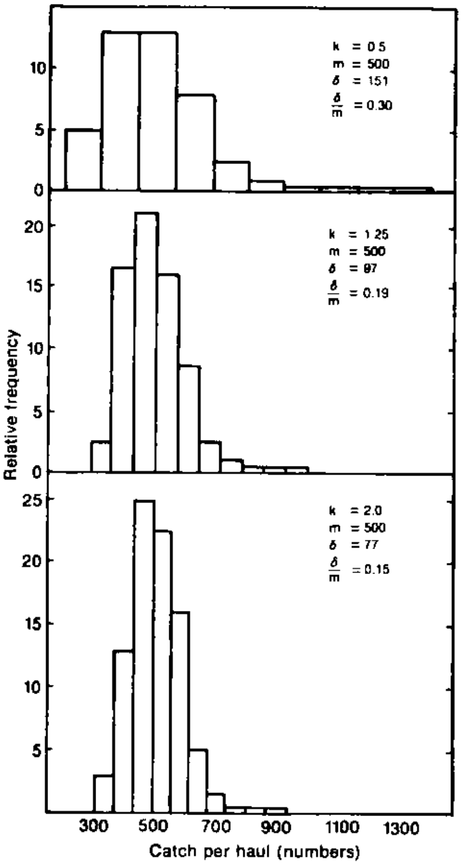

Fig. 2. Frequency distribution of the abundance index resulting from simulation of the negative binomial distribution (n = 20, m = 500).

TABLE 4. Estimates of parameters of the negative binomial distribution applied to silver hake survey data for Emerald Deep, 1972-76.

Year	Mean catch per haul (m)	Standard error (δ_m)	Negative binomial (k)	Standard error (δ_k)	Difference in third moments[a] ($T \times 10^9$)	Standard error of $T \times 10^9$
1972	885	205	0.98	0.45	-0.407	1.20
1973	858	190	1.02	0.45	-0.005	0.98
1974	1,292	195	2.32	0.90	-0.510	0.64
1975	2,635	558	1.11	0.48	-4.022	23.46
1976	1,507	330	1.04	0.46	-1.270	5.05

[a] See text for explanation.

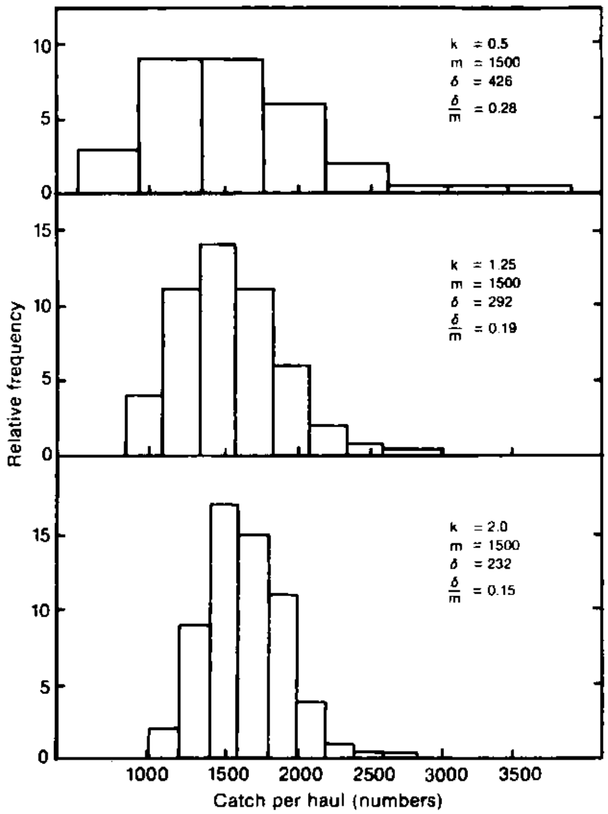

Fig. 3. Frequency distribution of the abundance index resulting from simulation of the negative binomial distribution (n = 20, m = 1,500).

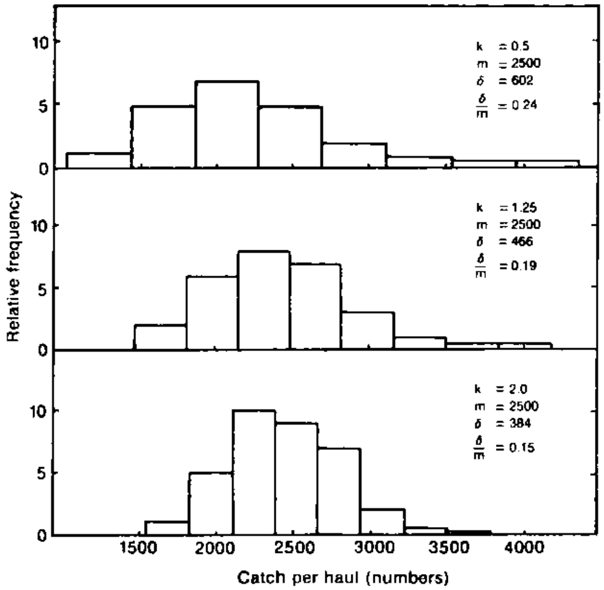

Fig. 4. Frequency distribution of the abundance index resulting from simulation of the negative binomial distribution (n = 20, m = 2,500).

from this analysis are as follows:

a) The distribution of the mean catch per haul is clearly asymmetrical, the asymmetry decreasing with increase in the parameter k and extending the increase in m.

b) The range of positive deviations from the mode significantly exceeds that of negative deviations.

c) The interval between the possible estimates of the "observed" abundance index is widened with increase in n and reduced with increase in k.

One of the problems to be solved by the method of statistical simulation was to determine the frequency of cases in which the calculated mean catch per haul fell outside of the 95% confidence interval defined by 2δ on either side of the mean distribution. As is evident from the results, the number of such cases range from 6 to 10%. The practical implication of this is that estimate of the abundance index will deviate significantly from the mean in approximately 1 case out of 10. This should be kept in mind when the sequence of the abundance indices for a number of years is compared, as in Fig. 1.

Using the parameters calculated for the 1975 survey data for silver hake in the Emerald Deep area (Table 4), computer simulations aimed at studying the variation in the accuracy of the abundance index by varying the number of hauls per survey were made. The results of the calculations for 20, 50, 100 and 200 hauls are shown in Fig. 5.

The distribution continues to be asymmetrical with 50 hauls but more closely approximates the normal curve for 100 and 200 hauls. The accuracy of the abundance index decreases from about 40% for 20 hauls per survey to about 25% for 50 hauls per survey. The accuracy increases very slowly with further increase in the number of hauls, declining to about 10% for 200 hauls. It is evident therefore that increasing the number of hauls per survey is not an efficient way to increase the accuracy of the abundance index, a conclusion which is consistent with that of Grosslein (1971).

Conclusions

1. The coefficient of variation of the abundance index for silver hake from surveys in the Emerald Deep area is about 20% for the actual catch-per-haul data.

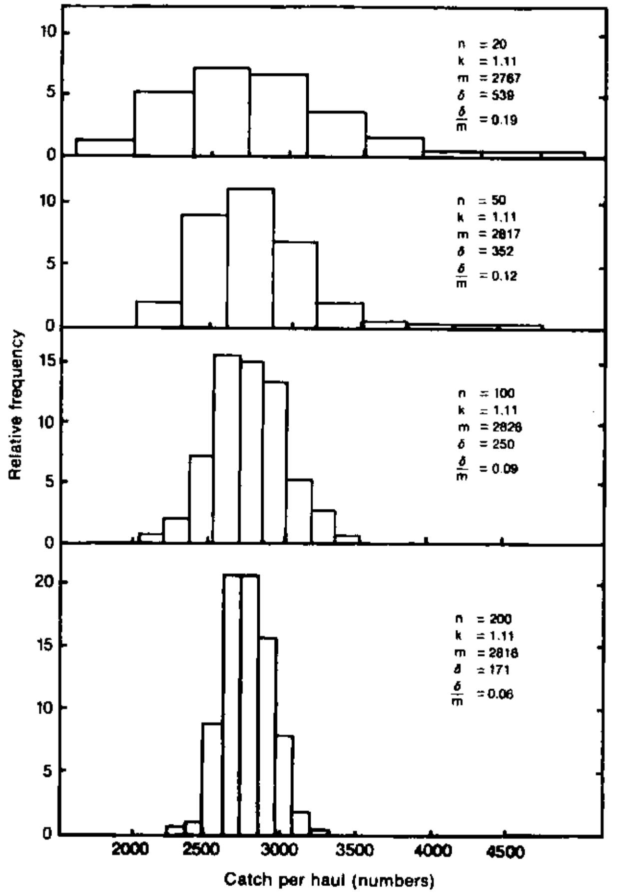

Fig. 5. Frequency distribution of the abundance index resulting from simulation of the negative binomial distribution for different numbers of hauls (m = 2,800).

2. Comparison of abundance indices from USSR and Canadian surveys and from virtual population analysis indicates that relatively large discrepancies in stock size estimates would result from the application of these time series of observations.

3. Analysis of the frequency distribution of the catch-per-haul data indicates consistency with the hypothesis of a negative binomial distribution, suggesting the usefulness of the method for analyzing the accuracy of abundance indices based on survey data.

4. Computer simulation studies revealed that increasing the number of hauls per survey is not a very efficient way of improving the accuracy of the abundance index.

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Food and Feeding of the Short-Finned Squid, *Illex illecebrosus*, During its Seasonal Occurrence in the Newfoundland Area[1]

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Abstract

The high percentage of empty stomachs generally found in squid caught in the Newfoundland area is inconsistent with the observation that their occurrence in this area is primarily the result of a feeding migration and with the fact that they grow rapidly while in the area. Samples collected from offshore areas in May and June have a higher incidence of crustacean remains than fish remains in the stomachs. Feeding conditions appear to improve somewhat when squid first migrate inshore and their diet changes to mainly fish (capelin). However, the incidence of fish remains in the stomachs declines from August to November and the incidence of squid remains (cannibalism) increases, indicating a deterioration in feeding conditions over this period. Squid collected from the offshore area in November-December have a higher incidence of crustacean remains than fish remains in their stomachs, and both the incidence of cannibalism and the percentage of empty stomachs is much lower than for the inshore samples collected during approximately the same period, indicating that feeding conditions improve considerably as squid move offshore in the autumn.

Introduction

During the course of its migratory cycle, the short-finned squid, *Illex illecebrosus*, spends up to 6 months in Newfoundland inshore waters. This inshore migration begins with the appearance of small squid on the Grand Bank in May (Hodder, 1964; Mercer and Paulmier, MS 1974). They grow rapidly and reach large sizes by October and November before migrating offshore (Squires, 1957). Their distribution in inshore waters varies from year to year but is usually quite widespread, and, with such an extended occurrence in the area, their feeding requirements (related to increasing size) and the feeding conditions encountered would be expected to vary considerably.

The purpose of this paper is to examine the variation in feeding activity and in the diet of squid throughout the period of its occurrence in two widely separated inshore areas. In addition, the role of *Illex illecebrosus* in the food chain is reviewed, on the basis of previously published information dealing with various aspects of the trophic relationships of this species.

Materials and Methods

In 1967, 16 samples of squid were obtained during July-November at Holyrood on the east coast of Newfoundland and 11 samples during August-October at Rencontre West on the south coast. All samples were taken from commercial catches and ranged from 77 to 492 squid (average 219 per sample). In addition, samples were obtained from cruises of *A. T. Cameron* on the southern part of the Grand Bank during 14 November-5 December 1967 and 30 May-3 June 1970. Part of the biological sampling routine was the examination of stomachs which included estimates of stomach fullness and cursory examination of stomach contents. The fullness of the stomachs was recorded according to the scale: empty, ¼ full, ½ full, and full. The stomach contents were usually quite mutilated and no attempt was made at detailed identification of the food items. However, the most common items observed were euphausiids, amphipods, compound eyes, otoliths, scales, fish eggs, and squid suckers and beaks, and these were grouped into crustacean, fish and squid remains for the purpose of this study.

Results and Discussion

Inshore squid samples

The percentage of empty stomachs in the Holyrood samples fluctuated between 57 and 81% but showed a declining tendency during the course of the July-November period (Fig. 1). At Rencontre West, this percentage ranged from 35 to 75% but the pattern of variation over the sampling period was very different. In this area the percentage of empty stomachs increased rapidly from early August to mid-September and decreased in October. Such a large increase

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[1] Submitted to the February 1978 Special Meeting of STACRES as Res. Doc. 78/II/7.

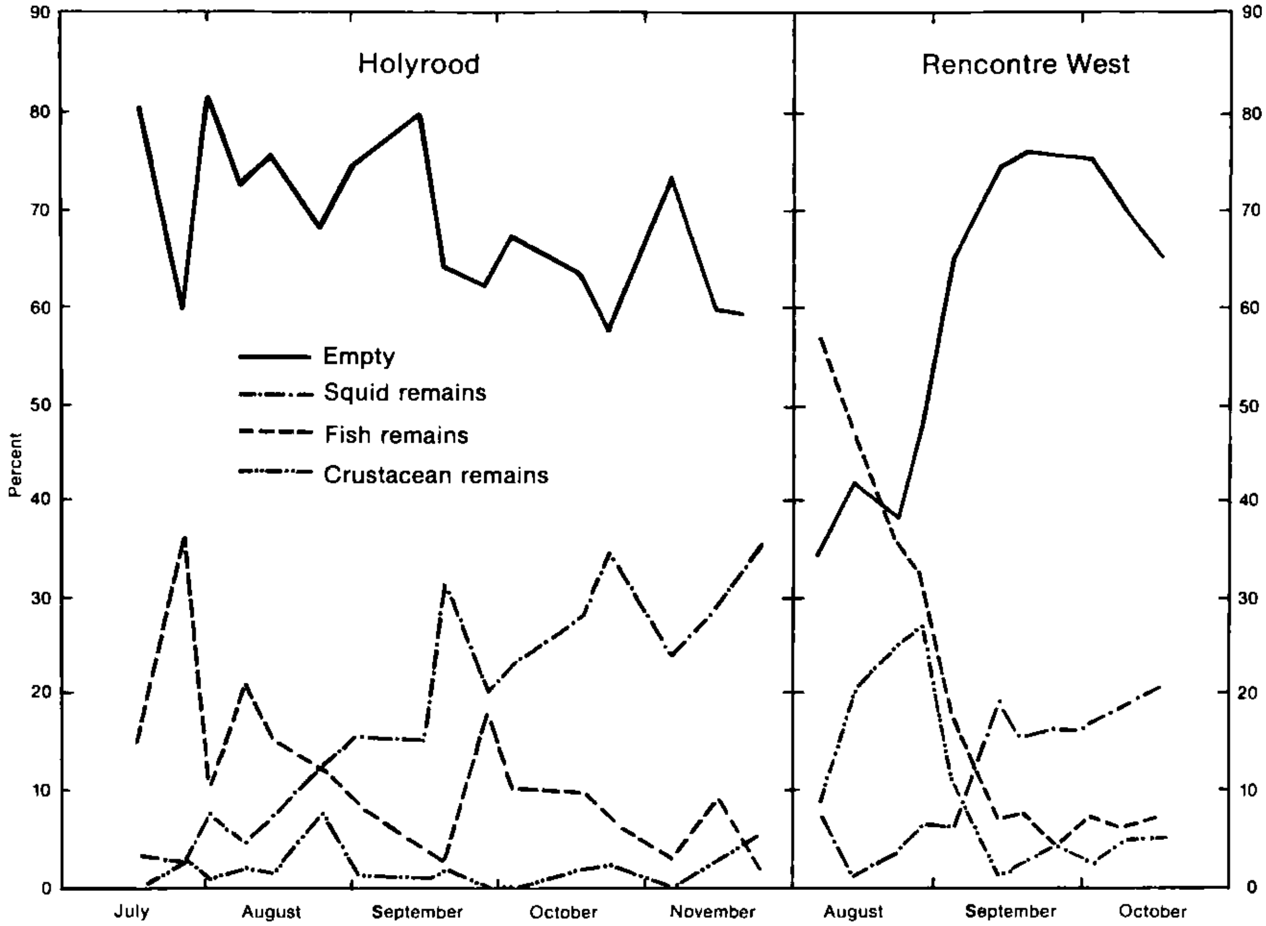

Fig. 1. Percentage of empty stomachs and incidence of various food remains in partially full and full stomachs of squid collected from Newfoundland inshore waters at Holyrood in July-November and at Rencontre West in August-October 1967.

suggests a sudden decline in the availability of food. The generally high percentages of empty stomachs observed in 1967 do not agree with the observations of Squires (1957, 1967) that the occurrence of squid in the Newfoundland area is primarily a feeding migration (as opposed to a spawning migration).

For both the Holyrood and Rencontre West samples, the percentages of full and ½ full stomachs among those which contained food tended to decrease over the sampling period and the percentage of ¼ full stomachs increased (Fig. 2), the trends being more pronounced in the Rencontre West samples. This appears to indicate that the level of feeding activity declines over the July-November period. However, squid grow rapidly over this period, and the actual volume of food in a ¼ full stomach of a large squid taken late in the year may be more or less equivalent to that in a full stomach of a small squid taken in the early part of the season. Since the larger squid require a larger volume of food to achieve satiation, it appears obvious that feeding activity does actually decline in relation to the increasing size of the animals. This may be related to a gradual transition from a predominately invertebrate diet in small squid to a predominately fish diet in large squid (Squires, 1957) and very likely to a generally lower availability of the latter.

In view of the observation by Squires (1957) that a gradual shift from an invertebrate to a fish diet occurs as the squid increase in size, one would have expected to find a declining incidence of crustacean remains and an increasing incidence of fish remains over the July-November period, but this was not the case. In the Holyrood samples, there was a low incidence of crustacean remains throughout the period and the incidence of fish remains declined from about 20% in July-August to about 5% in November (Fig. 1). At Rencontre West, on the other hand, the incidence of fish remains in the stomachs dropped sharply from nearly 60% in early August to less than 10% in September and October, whereas the incidence of crustacean remains increased during August and then declined sharply to low levels in the autumn. This rapid

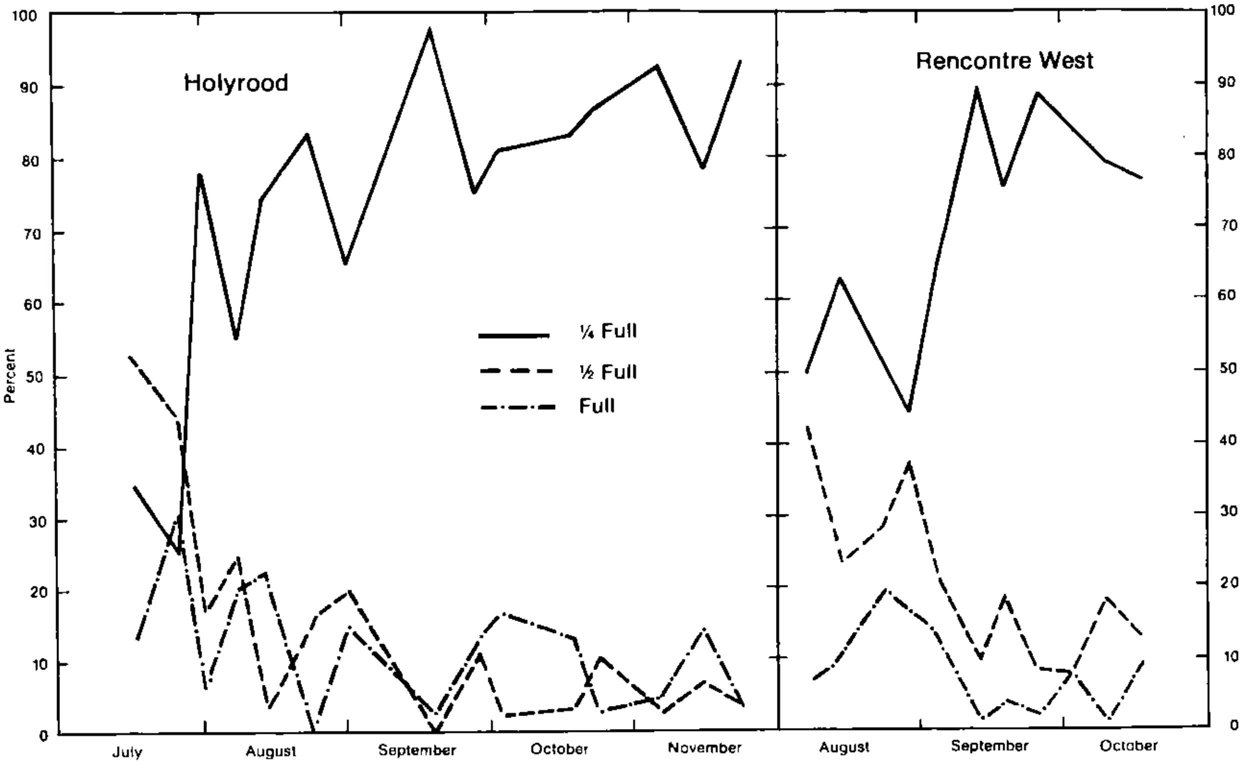

Fig. 2. Percentage of full, ½ full and ¼ full stomachs of squid containing food, collected from Newfoundland inshore waters at Holyrood in July–November and at Rencontre West in August–October 1967.

decrease in the incidence of both fish and crustacean remains coincides with the sharp increase in the percentage of empty stomachs in the Rencontre West area.

The incidence of cannibalism increased in both areas throughout the period of the study (Fig. 1). At Holyrood, squid remains were present in less than 4% of the stomachs taken in mid-July but were found in 35% of the stomachs in late November. At Rencontre West, the incidence of squid remains in the stomachs increased from about 2% in mid-August to 20% in October.

Offshore squid samples

The percentage of empty stomachs in the spring (May–June) offshore sample was relatively high (66%) and the incidence of crustacean remains in the stomachs containing food was higher (19%) than the incidence of fish remains (11%). Feeding conditions appear to improve as squid move inshore in early summer and change to a fish diet. The percentage of empty stomachs in the autumn (November–December) offshore sample was much lower (32%) than that for the inshore samples taken in late November (60%), and the incidence of both crustacean remains (43%) and fish remains (27%) was much higher. This, together with the low incidence of cannibalism (3% in the offshore sample compared with 35% in the inshore sample), indicates much better feeding conditions for squid in the offshore areas in the autumn. The incidence of cannibalism in the spring offshore sample was also very low (3%), suggesting that the schooling and feeding behaviour of squid on the offshore banks during their migration to and from the inshore areas is quite different from that during their presence in inshore waters.

Review of Predator-Prey Relationships in Squid

Squid as a predator

Mercer and Paulmier (MS 1974) list 10 taxa which form the principal components of the diet of *Illex illecebrosus* in the northern part of its range. These are Chaetognatha, Pteropoda, Cephalopoda, Ostracoda, Copepoda, Isopoda, Amphipoda, Euphausiidae, Decapoda (Natantia) and Teleostei. These authors have also identified many of the food items to the species level. Large differences in stomach contents were found in samples from different areas. On the Scotian Shelf, amphipods (mainly *Phronima atlantica* and *Parathemisto* spp.) and copepods (mainly *Euchirella rostrata* and *Candacia armata*) were the most important food items, whereas on the Grand Bank euphausiids (mainly *Meganyctiphanes norvegica*) occurred most frequently in the stomachs. Mercer and Paulmier (MS 1974) suggest that squid may feed selectively, since the copepods which predominate in the plankton of these areas (i.e. *Calanus finmarchicus* and *Pseudocalanus minutus elongatus*) were rarely found in the stomach contents.

The food items in squid stomachs collected in inshore Newfoundland waters also vary from area to area. In August 1964, squid in Placentia Bay were feeding primarily on crustaceans (unidentified) and to a much lesser extent on fish and squid, whereas at Holyrood in Conception Bay they were feeding on fish and squid but not on crustaceans (Mercer, MS 1965). Mercer also found green algae in a few stomachs taken at Holyrood. A high incidence of cannibalism is evident in samples from most areas (Squires, 1957; Mercer, MS 1965; Mercer and Paulmier, MS 1974). However, cannibalism may not be as prevalent as these samples indicate, since captured squid attack anything with which they come in contact, and this may account for much of the squid remains found among their stomach contents (Mercer, MS 1965). Nevertheless, the widespread incidence of squid remains in their stomachs suggests that cannibalism does exist in this species and may at times be an important part of their feeding behaviour.

Squires (1957) found a striking change in the food of squid as they increased in size. Small squid fed primarily on invertebrates (mainly euphausiids) and to a small extent on fish. As the squid increased in size, the incidence of fish remains in the stomachs gradually increased and fish predominated in the diet of larger animals. However, Squires combined samples collected over a 6-year period from the Grand Bank and inshore Newfoundland areas, and this would have masked any size-diet relationship. It seems more likely that squid feed opportunistically. The fish remains found in squid stomachs by Squires (1957) were identified as capelin, redfish, cod, haddock, mailed sculpin and small flounders. He also noted three invertebrate taxa, namely Gastropoda, Polychaeta and Mysidacea, not listed by Mercer and Paulmier (MS 1974).

Squid as prey

A major predator of *Illex illecebrosus*, at least during the 5–6 month period of its occurrence in Newfoundland waters each year, are the pilot whales, *Globicephala melaena*, which feed almost exclusively on squid (Squires, 1957; Sergeant, 1962). Mercer (1975) estimated the consumption of squid by a population of 50,000 pilot whales to be 166,000–249,000 metric tons during about 100 days when they are inshore and the annual consumption (assuming that pilot whales feed on these squid throughout the year) to be 605,900–908,350 tons. Squid and pilot whales are seasonal migrants to Newfoundland inshore waters, the two arriving and departing almost simultaneously (Mercer, 1975). This inshore-offshore migration of pilot whales appears to be in pursuit of squid, and it seems possible that this predator-prey relationship is maintained throughout the year, although nothing is known about the feeding of pilot whales in offshore waters (Sergeant and Fisher, 1957).

Squid also form a major part of the diet of bluefin tuna, *Thunnus thynnus*, when they occur inshore at Newfoundland during the summer months (Butler, 1971). However, *Illex illecebrosus* has not been found in the stomach contents of seven tuna species (including the bluefin) from elsewhere in the Atlantic Ocean (Dragovich, 1969). Other fish species reported as predators of *Illex illecebrosus* are silver hake, *Merlussius bilinearis*, and red hake, *Urophycis chuss* (Vinogradov, 1972) and spiny dogfish, *Squalus acanthias* (Templeman, 1944).

Squid commonly school at the surface and undoubtedly provide an important source of food for a variety of seabirds. Vovk (1974) reports different species of seabirds having been observed feeding on the long-finned squid, *Loligo pealei*. Although references to similar observations for *Illex illecebrosus* were not found during this review, seabirds which probably prey quite heavily on *Illex* are the greater shearwater, *Puffinus gravis*, the sooty shearwater, *Puffinus griseus*, the fulmar, *Fulmarus glacialis*, the northern gannet, *Morus bassanus*, and larger seagulls.

General trophic interrelationships

In a general way the trophic interrelationships of *Illex illecebrosus* are similar to those described for the long-finned squid, *Loligo pealei* (Vovk, 1974). The food of *Illex illecebrosus* includes organisms from three trophic levels: primary consumers (copepods, chaetognaths, euphausiids, etc.), secondary consumers (larger euphausiids, shrimp, amphipods, capelin, other squid, etc.), and tertiary consumers (redfish, cod, haddock, other squid, etc.). The incidence of green algae in squid stomachs was very low (Mercer, MS 1965), and such occurrences are most likely due to change than to active feeding.

This squid species in turn is preyed upon by a number of tertiary consumers. It is the most important food item of pilot whales and is very important in the diet of bluefin tuna, at least when the latter occur in the Newfoundland area. Squid are often eaten by silver and red hake and occasionally by dogfish. Cannibalism also appears to be a fairly common occurrence in *Illex illecebrosus*. In addition to those mentioned here, many other species of fish and marine mammals and a variety of seabirds undoubtedly include squid in their diets.

The role of *Illex illecebrosus* within the second and third trophic levels is quite clearly that of a predator. Within the fourth trophic level its primary role is that of a prey species, although it may also function as a predator and as a competitor. The short-finned squid is a highly migratory species and undoubtedly covers a very extensive depth range over the course of its migrations. Consequently, the structure of its trophic relationships would be expected to be quite variable throughout its migratory cycle.

The annual production of *Illex illecebrosus* in the Northwest Atlantic is estimated to be in the order of several hundred thousand tons (Mercer, 1975), and its role in the transmission of energy through the food chain to the higher trophic levels is considered to be a major one.

Acknowledgement

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Feeding of Short-Finned Squid, *Illex illecebrosus*, and Long-Finned Squid, *Loligo pealei*, off Nova Scotia and New England, 1974-75[1]

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Abstract

Analysis of the stomach contents of the short-finned, *Illex illecebrosus*, and long-finned, *Loligo pealei*, squids taken in 1974 and 1975 on the continental slope of Nova Scotia and New England indicated that crustaceans, fish and squid were the most important components of the diet of these species. The proportions of the three major food components in the stomachs varied by area and season for each species. On the average, crustaceans, fish and squid constituted 51, 25 and 24% respectively of the diet of short-finned squid and 20, 53 and 26% of the diet of long-finned squid. Both species of squid seem to feed more intensively at night than in the daytime, but the evidence for the short-finned squid is less convincing than that for the long-finned squid. The daily ration of large short-finned squid (19-25 cm) was estimated to be 5.8% of the body weight. Estimates of the daily ration for small (8-15 cm) and large (16-30 cm) long-finned squid were 3.8 and 3.2% of the body weight respectively. Cannibalism is apparently a common phenomenon in both species.

Introduction

Two species of squids, the short-finned, *Illex illecebrosus*, and the long-finned, *Loligo pealei*, are of commercial importance in the Northwest Atlantic. Although subject to fluctuations in abundance from year to year, large numbers of short-finned squid are usually found in late spring and early summer on the continental shelf from southern New England (ICNAF Statistical Area 6) to Newfoundland (Subarea 3), where they feed intensively and grow rapidly during the summer and then migrate from the shelf in late autumn to oceanic spawning areas. In the summer of 1976, for example, on the basis of data from a trawling survey by the R/V *Belogorsk*, the biomass of short-finned squid on Georges Bank was estimated to be about the same as that for all fish species in the area. The long-finned squid, on the other hand, are usually abundant from late autumn to spring on the shelf from Georges Bank to southern New England (Subarea 5 and Statistical Area 6).

Due to their high abundance, these squids support a substantial commercial fishery which has expanded from an average annual catch of 10,000 tons during 1965-70 to 125,000 tons in 1977. These species, therefore, play an important role in the food chain, and studies on their feeding patterns are necessary for understanding their predator-prey relationships.

Materials and Methods

Data for the feeding studies on squid were collected during trawling surveys of the R/V *Khronometer* and *Belogorsk* in August-November 1974 and in August 1975 on the continental shelf off Nova Scotia and New England (Fig. 1). The diurnal feeding pattern of the short-finned squid was investigated from samples taken on the northwest slope of Georges Bank during 1-4 August 1975 and of the long-finned squid from samples taken in an area south of Nantucket Island on 18-19 September 1975.

Two size groups of long-finned squid were sampled (8-15 cm and 16-30 cm mantle length), the first group being considered representative of immature and the second group of mature specimens (Vovk, 1972a). The catches of short-finned squid on the shelf consist almost entirely of immature specimens, maturing squid occurring infrequently in the autumn during their migration from the shelf areas. Consequently, the size groups of short-finned squid were selected with regard to the predominance of food organisms in the stomachs: crustaceans in the smaller individuals (10-18 cm mantle length) and mainly fish in the larger individuals (19-25 cm). Each sample consisted of 20 specimens, or less if the required number could not be obtained.

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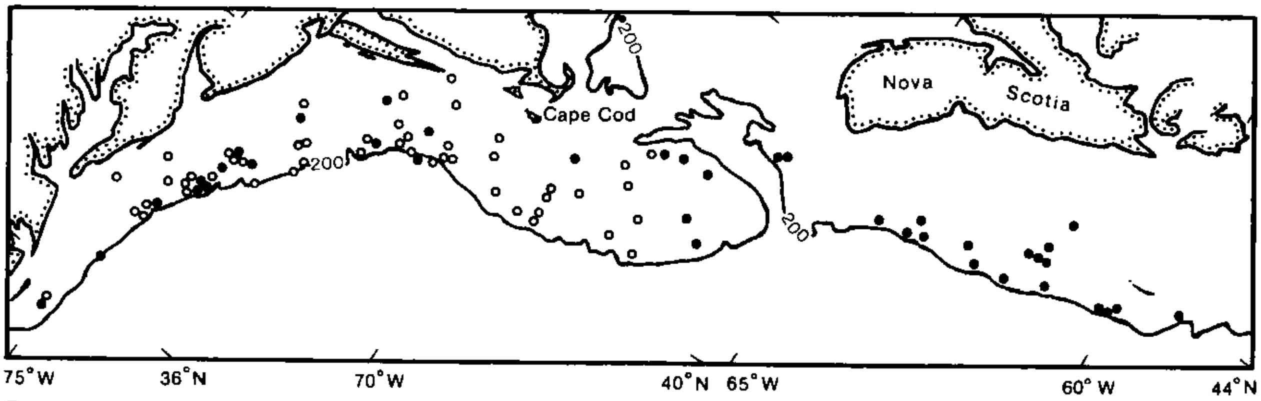

Fig. 1. Location of sampling stations off Nova Scotia and New England where short-finned (closed circles) and long-finned (open circles) squids were taken for feeding studies.

Most of the samples were frozen immediately after collection and the stomach contents examined later in the laboratory after defrosting. A few samples initially preserved in 10% formalin were soaked in water for a day prior to examination in the laboratory. Upon dissection of the specimens of each size group, the number of empty stomachs was recorded, and the contents of stomachs containing food items were placed in a dish and separated into various components which were then weighed to determine the relative composition of the food. Since the food items were reduced to small fragments by the beak and radula of squid, identification of the various items was often very difficult. The taxonomic groups into which the food components were divided are listed in Table 1. Fish remains could often be identified from the structure of otoliths and squid from the presence of beaks and suckers.

TABLE 1. Food composition (% by weight) of short-finned and long-finned squids in the Northwest Atlantic (Subareas 4 to 6) based on samples taken in 1974 and 1975.

Food items in stomachs	Short-finned squid	Long-finned squid
Mysids	0.5	—
Gammarids	0.1	1.8
Meganyctiphanes sp.	0.5	—
Euphausiids	25.4	0.3
Pandalus montagui	0.1	—
Crabs	0.2	0.1
Decapods	5.1	9.8
Unidentified crustaceans	18.7	8.4
Total crustaceans	**50.6**	**20.4**
Squid remains	24.0	26.2
Myctophids	2.9	—
Silver hake	7.1	4.2
Unidentified fish	15.4	49.2
Total fish and squid	**49.4**	**79.6**
No. of specimens examined	980	1,323

The feeding index was determined from the ratio of the weight of food in the stomachs to the body weight of the squid (Anon., 1974).

Results

Food components in the diet of squids

A summary of the data obtained from the analysis of the stomachs of 980 short-finned squid and 1,323 long-finned squid taken on the continental shelf off Nova Scotia and New England is given in Table 1. Crustaceans, squid and fish constituted the major food components of the diet of both species but in different proportions. Euphausiid (25% by weight) fish (25%), and squid (24%) remains were commonly found in the stomachs of short-finned squid, with crustaceans forming slightly more than 50% of the food components. In the long-finned squid, on the other hand, the major food items were fish (53%) and squid (26%), with crustaceans constituting only 20% of the diet. Mercer and Paulmier (MS 1974) listed 10 types of food organisms found in the stomachs of *I. illecebrosus* on the Scotian Shelf in May–June and suggested that this species may feed rather selectively, but no evidence of selective feeding is indicated from the results of our studies.

Illex illecebrosus. Although the small (10–18 cm) and large (19–25 cm) short-finned squid consumed on the average relatively equal proportions of crustaceans (45 and 47% by weight) and of squid and fish combined (55 and 53%), considerable differences were observed in the food composition of these two size groups from different areas (Table 2). For example, on Georges Bank in August 1975, squid and fish constituted 55% of the diet of small squid and 94% of the diet of large squid. A similar pattern was observed in August 1974 on Emerald Bank where the corresponding values were 49 and 93%. In September 1974 to the south of Long Island, squid constituted the major food item (42%) of small squid, whereas the large squid fed mainly on fish (64%). Similarly in August 1974 on Nantucket Shoals, 47% of the food of small individuals consisted of squid, whereas the large squid fed mainly on crustaceans and fish. The prevalence of squid remains in the stomachs of small *I. illecebrosus* may be explained by the fact that very small (3–10 cm) long-finned squid, *L. pealei*, are usually abundant in these areas during the same period (Vinogradov, 1970). In any case, cannibalism appears to be quite common in most of the areas. However, in the Browns Bank area, crustaceans constituted 100% of the food of the large squid in August of 1974 and 1975. This may be considered an exception to the general pattern, indicating the absence of suitable fish food and the availability of large concentrations of euphausiids and other crustaceans accessible as food for squid during the period. A similar phenomenon was observed by Ennis and Collins (1979) in the Newfoundland area.

The feeding index of short-finned squid varied greatly by area and season (Table 2). The lowest value (0.4%) was observed on Emerald Bank in August 1975 and the highest value (29.4%) on Browns Bank in August 1974. Correspondingly, the proportions of empty stomachs in large squid were 74% and 0% respectively. On the average, small squid had a lower feeding index (4.0%) and a higher proportion of empty stomachs (36%) than the corresponding values for large squid (8.8% and 26% respectively). Although the feeding indices for short-finned squid are not very different from those for silver hake (Vinogradov, 1975), the daily food consumption by squid is undoubtedly higher due to greater frangmentation of food organisms being eaten and more rapid digestion in the course of 6–8 hours. This results in a high growth rate during the feeding period from June to October, averaging 2 cm or more in mantle length per month (Konstantinov and Noskov, 1973; Mercer, MS 1975; Tibbetts, 1977).

Loligo pealei. On the average for all areas (Table 3), crustaceans, fish and squid constituted 40, 40 and

TABLE 2. Food composition (% by weight) of short-finned squid by area, season and size group for the Northwest Atlantic, 1974-75.

	Emerald Bank			Browns Bank		Georges Bank		Nantucket	South of Long Island			
Food items in stomachs	May 1974	Aug 1974	Aug 1975	Aug 1974	Aug 1975	May 1974	Aug 1975	Aug 1974	Aug 1974	Sep 1974	Oct 1974	Average for all areas
						Small Squid, 10–18 cm Mantle Length						
Mysids	—	—	—	—	—	—	39	—	—	—	—	5
Gammarids	—	—	—	—	—	—	6	—	—	—	—	1
Meganyctiphanes sp.	—	—	—	—	—	—	—	—	—	—	—	—
Euphausiids	—	1	—	—	—	—	—	—	—	—	—	+
Pandalus montagui	—	—	—	—	—	—	—	—	—	—	—	—
Crabs	—	—	—	—	—	—	—	—	—	6	—	1
Decapods	—	50	—	—	—	—	—	53	—	21	—	15
Unidentified crustaceans	—	—	80	—	—	—	—	—	100	1	—	23
Total crustaceans	—	**51**	**80**	—	—	—	**45**	**53**	**100**	**28**	—	**45**
Squid remains	100	47	20	—	—	100	6	47	—	42	—	45
Myctophids	—	—	—	—	—	—	—	—	—	—	—	—
Silver hake	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified fish	—	2	—	—	—	—	49	—	—	30	—	10
Total fish and squid	**100**	**49**	**20**	—	—	**100**	**55**	**47**	—	**72**	—	**55**
No. of specimens examined	20	124	20	—	—	20	60	80	20	149	—	493
% with empty stomachs	30	27	70	—	—	20	47	34	30	40	—	36
Feeding index (%)	8.0	5.7	0.4	—	—	6.0	2.4	10.9	1.3	2.5	—	4.0
						Large Squid, 19–25 cm Mantle Length						
Mysids	—	—	—	—	—	—	—	—	—	—	—	—
Gammarids	—	—	—	—	—	—	+	—	—	—	—	+
Meganyctiphanes sp.	—	6	—	—	—	—	—	—	—	—	—	1
Euphausiids	—	—	—	100	30	—	—	—	—	36	—	18
Pandalus montagui	—	1	—	—	—	—	—	—	—	—	—	+
Crabs	—	—	—	—	—	—	—	—	—	—	—	—
Decapods	—	+	—	—	—	—	—	—	—	+	—	+
Unidentified crustaceans	—	—	100	—	70	—	6	60	—	—	10	27
Total crustaceans	—	**7**	**100**	**100**	**100**	—	**6**	**60**	—	**36**	**10**	**47**
Squid remains	100	37	—	—	—	—	50	—	—	1	—	21
Myctophids	—	—	—	—	—	—	16	40	—	3	—	6
Silver hake	—	24	—	—	—	—	—	—	—	28	—	6
Unidentified fish	—	32	—	—	+	—	18	—	—	32	90	20
Total fish and squid	**100**	**93**	—	—	+	—	**94**	**40**	—	**64**	**90**	**53**
No. of specimens examined	20	141	19	20	60	—	73	20	—	113	21	487
% with empty stomachs	55	26	74	0	28	—	40	0	—	19	0	26
Feeding index (%)	16.0	3.2	0.4	29.4	18.8	—	3.4	8.4	—	8.2	13.3	8.8

TABLE 3. Food composition (% by weight) of long-finned squid by areas, season and size group for the Northwest Atlantic, 1974-75.

	Georges Bank			Nantucket		South of Long Island	
Food items in stomachs	Aug	Oct	Nov	Aug	Oct	Sep	Average for all areas
	Immature Squid, 6–15 cm Mantle Length						
Gammarids	—	—	—	30	—	—	5
Euphausiids	—	—	—	8	—	—	1
Crabs	—	—	—	—	—	—	—
Decapods	100	—	—	16	—	14	21
Unidentified crustaceans	—	58	—	1	—	19	13
Total crustaceans	**100**	**58**	**—**	**55**	**—**	**33**	**40**
Squid remains	—	8	10	32	42	28	20
Silver hake	—	—	90	—	—	—	15
Unidentified fish	—	34	—	13	58	39	25
Total fish and squid	**—**	**42**	**100**	**45**	**100**	**67**	**60**
No. of specimens examined	40	140	20	135	40	324	699
% of empty stomachs	26	39	25	54	38	27	35
Feeding index (%)	1.8	2.3	18.6	1.7	3.0	2.5	2.7
	Mature Squid, 16–30 cm Mantle Length						
Gammarids	11	—	—	—	—	—	2
Euphausiids	—	—	—	—	—	—	—
Crabs	—	1	—	—	—	—	+
Decapods	54	2	—	—	—	10	14
Unidentified crustaceans	—	3	—	—	—	7	2
Total crustaceans	**65**	**6**	**—**	**—**	**—**	**17**	**18**
Squid remains	3	41	20	—	7	36	21
Silver hake	—	—	—	—	—	—	—
Unidentified fish	32	53	80	—	93	47	61
Total fish and squid	**35**	**94**	**100**	**—**	**100**	**83**	**82**
No. of specimens examined	99	167	16	—	40	302	624
% of empty stomachs	42	30	6	—	5	36	17
Feeding index (%)	1.9	2.1	1.7	—	7.4	1.7	2.3

20% respectively of the food of small squid, whereas the proportions of these food types in large individuals were 18, 61 and 21%. The food composition varied by area and season. In August and October 1974 on Georges Bank, small squid fed mainly on crustaceans (100 and 58% respectively), whereas in November the diet consisted almost entirely of juvenile silver hake (90%). For large squid in the same area, the proportions of fish and squid remains in the diet increased from 35% in August to 94% in October and to 100% in November, as the percentage of empty stomachs declined. On Nantucket Shoals in August, small squid fed mainly on crustaceans (55%), whereas in October fish (58%) and squid (42%) constituted the entire diet. The large squid in this area fed almost entirely on fish (93%). In the area south of Long Island, both small and large squid fed mainly on fish and squid, with crustaceans forming 33% of the diet of small squid and 17% of the diet of large individuals.

The feeding index of long-finned squid was on the average rather low, being only 2.7% and 2.3% for small and large individuals respectively (Table 3). However, on Georges Bank in 1974, the feeding index of small squid varied greatly from 1.8 in August to 18.6% in November, whereas that for large squid remained at about the same level (1.7-2.1%) during the period. According to Summers (1971), the monthly growth increments of this species range from 1.0 to 1.5 cm during the feeding period.

Variation in food composition with depth

Analysis of the food composition of *I. illecebrosus* by depth indicated that crustaceans became less important in the diet of small squid at the greatest depth range (151-365 m), being replaced by fish and squid (Table 4). However, the relative proportion of crustaceans in the diet of large individuals increased greatly (10 to 83%) with increasing depth as the importance of fish and squid as food items declined. The feeding index of both small and large squid, especially the latter, increased markedly with depth and the number of empty stomachs declined.

For *L. pealei*, the relative percentage of fish and squid remains in the stomachs of small individuals increased from 56 to 77% by weight as the importance of crustaceans in the diet and the relative number of empty stomachs declined (Table 4). The percentage of fish and squid remains in the stomachs of large individuals varied only slightly with depth (87–100%), and no significant change with depth was observed in the percentage of empty stomachs (30–35%) or in the feeding intensity (2.0–2.8%).

Diurnal feeding behaviour

Analysis of samples taken during a 3-day period in August 1975 at a station on the northwest slope of Georges Bank indicated that the feeding intensity of *I. illecebrosus* was highest during the night and lowest in the afternoon (Fig. 2). This observation is in agreement with that of Bradbury and Aldrich (1969) who reported that squid in captivity feed before daybreak. The analysis also showed that short-finned squid feed mainly on fish during the night and on crustaceans during the daytime, indicating that the nighttime is more favourable for squid predation on fish. From the available data for the 3-day period, the daily ration of large squid (19–25 cm) was estimated to be 5.8% of the body weight.

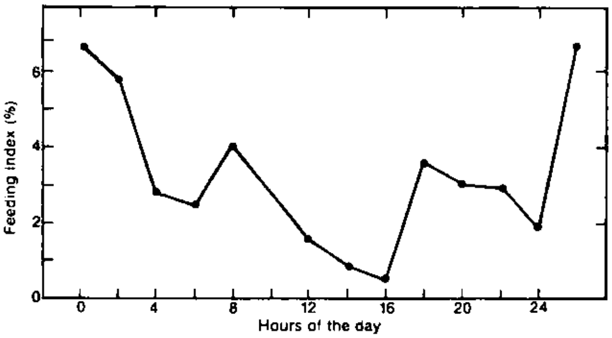

Fig. 2. Diurnal variation in the feeding intensity (index) of short-finned squid, based on data from hauls over 3 days at a station on Georges Bank in August 1975.

For *L. pealei*, analysis of data obtained during a 2-day period on Nantucket Shoals revealed no clear diurnal feeding pattern. However, it was observed that the most intensive consumption of food by large squid occurred during the evening (1800–2000 hr). During the autumn months, according to Vovk (1972b), *L. pealei* feed most intensively in the period from 1600 to 2000 hr. From the available data, the daily ration was estimated to be 3.8% of the body weight for small individuals (8–15 cm) and 3.2% for large individuals (16–30 cm).

Conclusions

1. Nearly 50% of the diet of both small and large short-finned squid, *I. illecebrosus*, consisted of crustaceans, the remaining food components being mainly squid in the smaller (10–18 cm) and fish in the larger (19–25 cm) individuals.

2. Long-finned squid, *L. Pealei*, in general fed mainly on fish, although crustaceans may form a significant part of the diet in the smaller individuals. Crustaceans, fish and squid constituted about 40, 40 and 20% respectively of the diet of the smaller (8–15 cm) individuals and

TABLE 4. Food composition (% by weight) of short-finned and long-finned squids by depth and size category. (For the short-finned squid, S = 10–18 cm and L = 19–25 cm mantle length; for the long-finned squid, S = 8–15 cm and L = 16–30 cm mantle length.)

	Short-finned squid						Long-finned squid					
	42–70 m		71–150 m		151–365 m		27–70 m		71–150 m		210–600 m	
Food items in stomachs	S	L	S	L	S	L	S	L	S	L	S	L
Mysids	19	—	—	—	—	—	—	—	—	—	—	—
Gammarids	3	+	—	—	—	—	10	1	—	—	—	—
Meganyctiphanes sp.	—	—	—	—	—	1	—	—	—	—	—	—
Euphausiids	—	—	—	29	1	38	—	—	—	—	13	—
Pandalus montagui	—	—	—	+	—	—	—	—	—	—	—	—
Crabs	—	—	—	—	14	—	—	—	—	—	—	—
Decapods	25	—	42	1	—	—	24	9	16	7	10	—
Unidentified crustaceans	—	10	6	6	—	43	10	2	17	6	—	—
Total crustaceans	**47**	**10**	**48**	**36**	**15**	**83**	**44**	**12**	**33**	**13**	**23**	—
Squid remains	24	2	51	36	26	12	26	20	15	39	40	11
Myctophids	—	9	—	4	—	2	—	—	—	—	—	—
Silver hake	—	—	—	16	—	—	—	17	27	—	—	—
Unidentified fish	29	79	1	8	59	3	30	51	25	48	37	89
Total fish and squid	**53**	**90**	**52**	**64**	**85**	**17**	**56**	**88**	**67**	**87**	**77**	**100**
No. of specimens examined	133	92	299	212	61	183	354	266	325	326	40	10
% with empty stomachs	43	32	32	24	39	27	41	35	28	34	5	30
Feeding index (%)	2.2	4.5	4.9	9.2	3.8	10.5	2.6	2.4	2.8	2.0	4.9	2.8

about 18, 61 and 21% of the diet of the larger (16-30 cm) specimens.

3. The daily ration of large *I. illecebrosus* (19-25 cm) was estimated to be about 5.8% of the body weight on Georges Bank in August 1975. Estimates of the daily ration for small (8-15 cm) and large (19-30 cm) *L. pealei* were 3.8 and 3.2% respectively on Nantucket Shoals in September 1975.

4. Both the short-finned and long-finned squids exhibit cannibalism in most of the areas and seasons for which data were available, with squid forming 24 and 26% of the diet respectively.

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Standardization of Data Collection for the Short-finned Squid, *Illex illecebrosus*[1]

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Abstract

Recognition of the need to standardize data collection for *Illex illecebrosus* has resulted in the development of procedures and standards for biological sampling, involving the collection of data on mantle length, body weight, sex, maturity and stomach fullness, so that an adequate data base can be established to provide for essential parameters for stock assessment.

Introduction

The fishery for the short-finned squid, *Illex illecebrosus*, in the Northwest Atlantic has developed rapidly in recent years, especially off the Canadian coast (Amaratunga *et al.*, MS 1978a, MS 1978b), where catches totalled 88,000 metric tons in 1977. A complete understanding of the biology and distribution of this species, much of which is unknown, is required for the proper management of the fishery. Field data are the major sources of information pertaining to age, growth and other related parameters of the population. Data are available on *Illex* from different areas for many years (Squires, 1957, 1967; Mercer, MS 1973, MS 1975; Mesnil, 1977; Tibbetts, 1977), but the corelation of data from these sources is difficult due to variation in methods of collection and presentation. The need to standardize data collection was recognized at a meeting of ICNAF's Standing Committee on Research and Statistics (STACRES) in February 1978, when procedures for biological sampling of *Illex* were adopted.

Two different life cycles have been proposed for *I. illecebrosus* (Squires, 1967; Mesnil, 1977). Both have been derived from interpretation of field data collected mainly during the fishing season from May to November, but no data are available for the critical maturation, breeding and recruitment phases of the life cycle. It is therefore important that extensive data be collected during the period from December to April in order to complete the picture. It is also important that standard criteria be used for data collection in order to facilitate data comparisons and simplify analyses.

Mercer (MS 1973) described an index of sexual maturity for male *Illex*, but similar information on maturation in females has not been available until recently (O'Dor *et al.*, 1977) when full maturation was observed in captive animals. A maturity index for females, including fecundity estimates, has been described from these laboratory observations and subsequent field samples (Durward *et al.*, 1979). Utilizing these maturity indices, the maturation process in both sexes can now be readily studied in the field.

In this paper, standard methods of data collection, applicable to both field and laboratory conditions, are described. The required morphometric measurements and observations are simple enough that they can be carried out by field personnel with a minimum of training.

Data Requirements

The procedures and standards presented in this paper were adopted by STACRES (ICNAF, 1978) as a general guide for the biological sampling of *I. illecebrosus*, involving the collection of data on mantle length, body weight, sex, maturity stages and stomach fullness. The systematic collection of these data will provide the foundation for subsequent research and standardization of information. Such a data base will provide the fundamental parameters for stock assessment and the formulation of management programs.

Length and weight measurements provide the basic data on age and growth for use in population models to estimate biomass and sustainable yield. Mantle length can be measured with a high degree of consistency by different observers in contrast to the

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[1] Submitted to the February 1978 Special Meeting of STACRES as ICNAF Res. Doc. 78/II/5.

variability associated with measurements involving the tentacles. Total body weight measurements should be taken when conditions permit, as such data when related to length allow the estimation of yield and stock size in numbers. Also, the weight of females is known to be related to fecundity (Durward *et al.*, 1979), and the utilization of biomass and fecundity data allows the estimation of the reproductive potential of the stock. Historical length and weight data may be used to assess seasonal and annual trends in stock composition.

Variation in the growth and maturity of males and females require that the sex be determined for all specimens sampled. Sex ratios and the sequence of changes in maturation during the life cycle are important in ascertaining the size and age at which sexual maturity is attained. Data on maturation may provide clues to the duration of the reproductive cycle and the time and location of spawning. Data on age and size at maturity may provide options for management as to the duration of the fishing season in order to conserve an adequate spawning stock.

Data on stomach contents and fullness allows the estimation of feeding patterns on a diurnal and seasonal basis. Correlation of these data with laboratory studies on feeding rates, food preference and growth efficiency may provide a means of assessing the interaction of squid with other species. Laboratory observations (O'Dor *et al.*, 1977) indicate that there is a complex social structure in schools of *Illex* which affect feeding rates in individuals. The presence of dominant members in the schools may relate to breeding patterns and the quality of the breeding stock. Correlation between size of individuals and their feeding frequency may help to clarify this behavioural component of the life cycle.

Standardization of Data Collection

Each sample should consist of at least 100 *Illex* randomly collected from the catch, and each data set

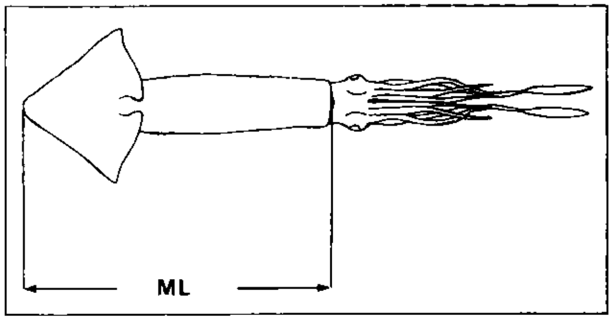

Fig. 1. Dorsal view of *Illex illecebrosus*. Dorsal mantle length (ML) is measured from the anterodorsal protuberance of the mantle to the apex of the tail fin.

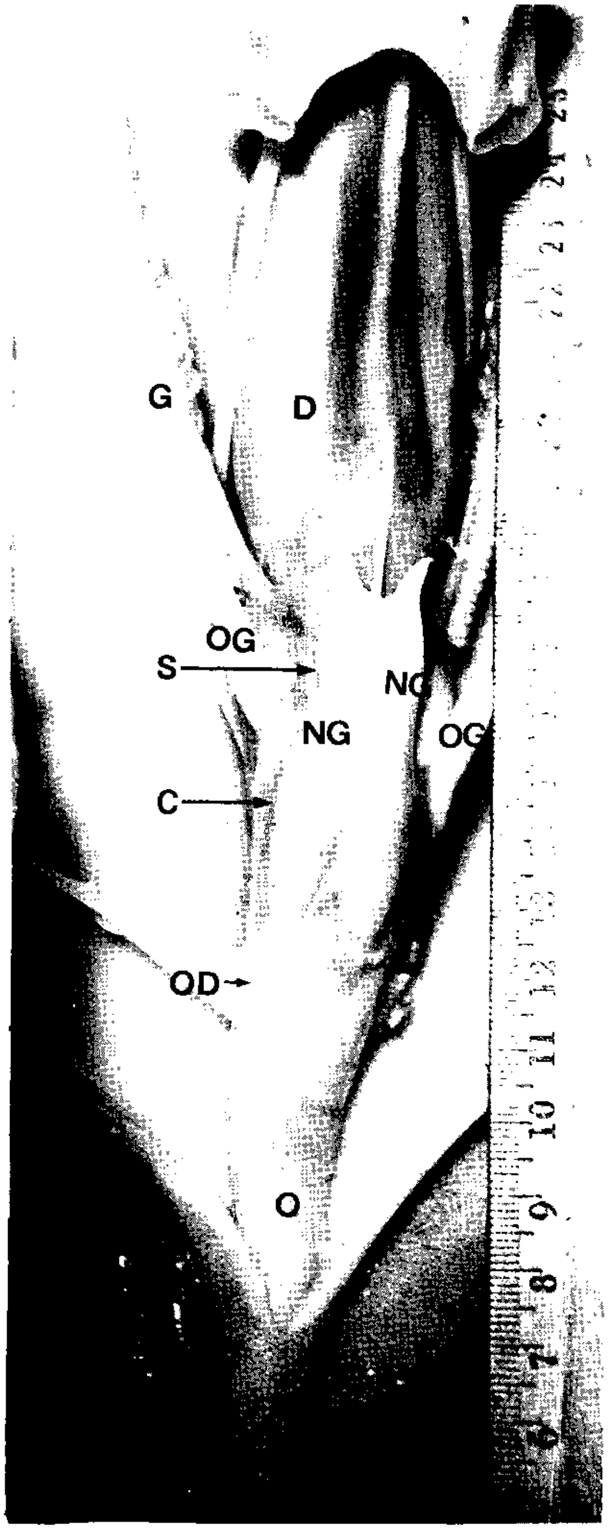

Fig. 2. General anatomy of the female *Illex illecebrosus*: C — caecum located under the posterior half of nidamental gland; D — digestive gland; G — gill; NG — nidamental gland; O — ovary; OG — oviducal gland; OD — oviduct (not yet formed but will develop in this area); S — stomach located under the anterior half of NG.

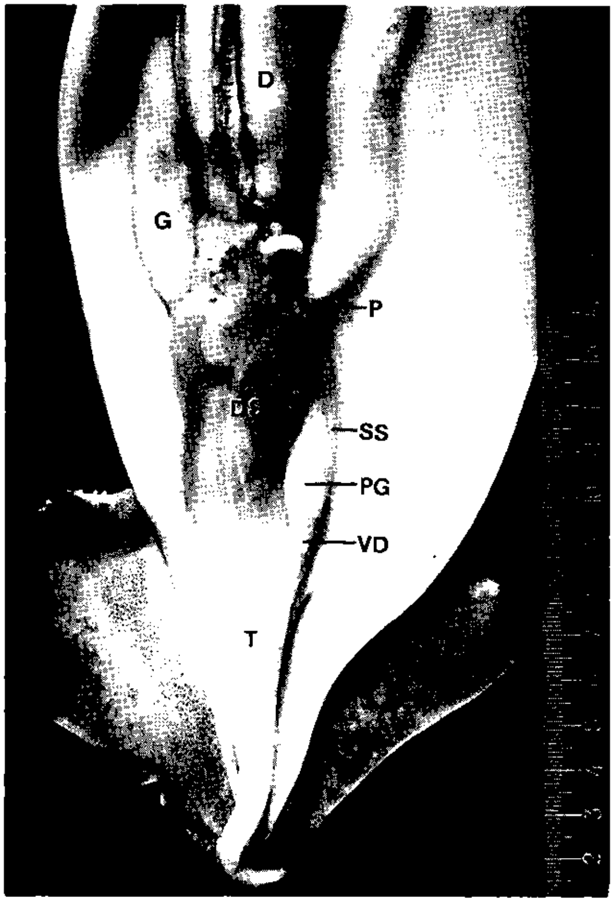

Fig. 3. General anatomy of the male *Illex illecebrosus*: D — digestive gland; DS — digestive system; G — gill; I — ink sac; P — penis; PG — prostate gland; SS — spermatophoric sac; T — testis; VD — vas deferens.

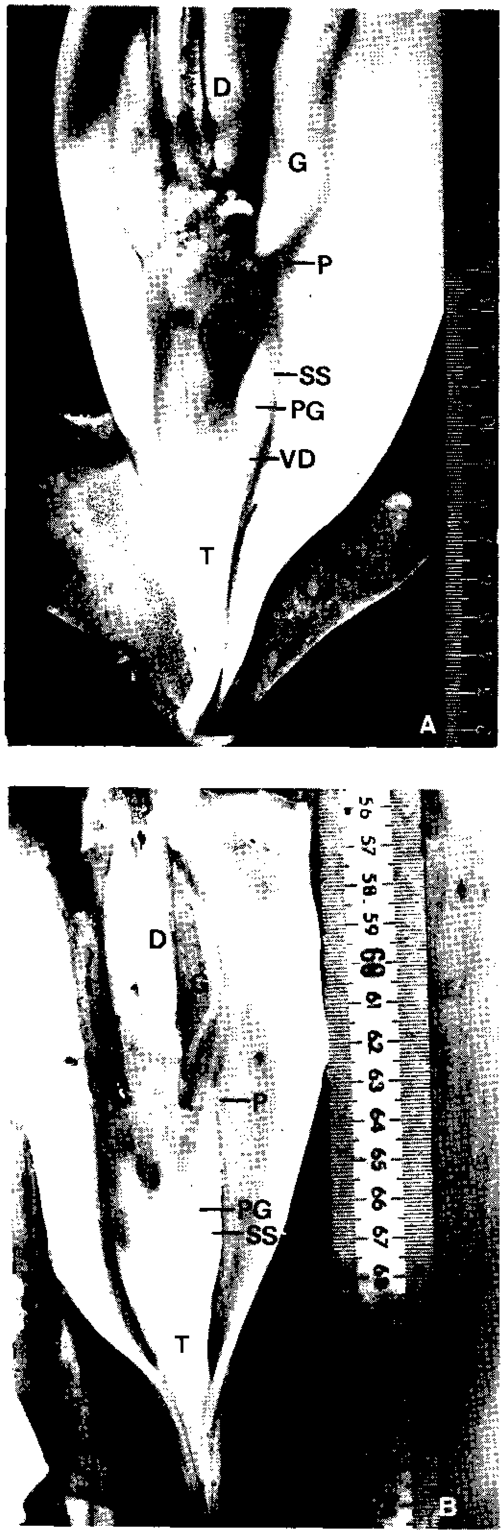

Fig. 4. Typical examples of male *Illex illecebrosus* in Stage 2 (A), and in Stage 3 (B). Symbols showing the various organs are the same as thosa defined in Fig. 3.

must necessarily include all relevant information from the vessel's logbook pertaining to the catch. In order to standardize the collection of both commercial and research samples, examination of the specimens should follow the procedures described below.

Dorsal mantle length

The mantle length should be measured from the anterodorsal protuberance of the mantle to the apex of the tail fin, as illustrated in Fig. 1. According to the requirements of STACRES (ICNAF, 1978), length composition data should be reported by ½-cm intervals for males and females separately.

Total body weight

The weight of each specimen in the fresh (wet) condition should be recorded to the nearest gram. It is important that excess water be drained from each specimen and from the weighing pan prior to each weight determination.

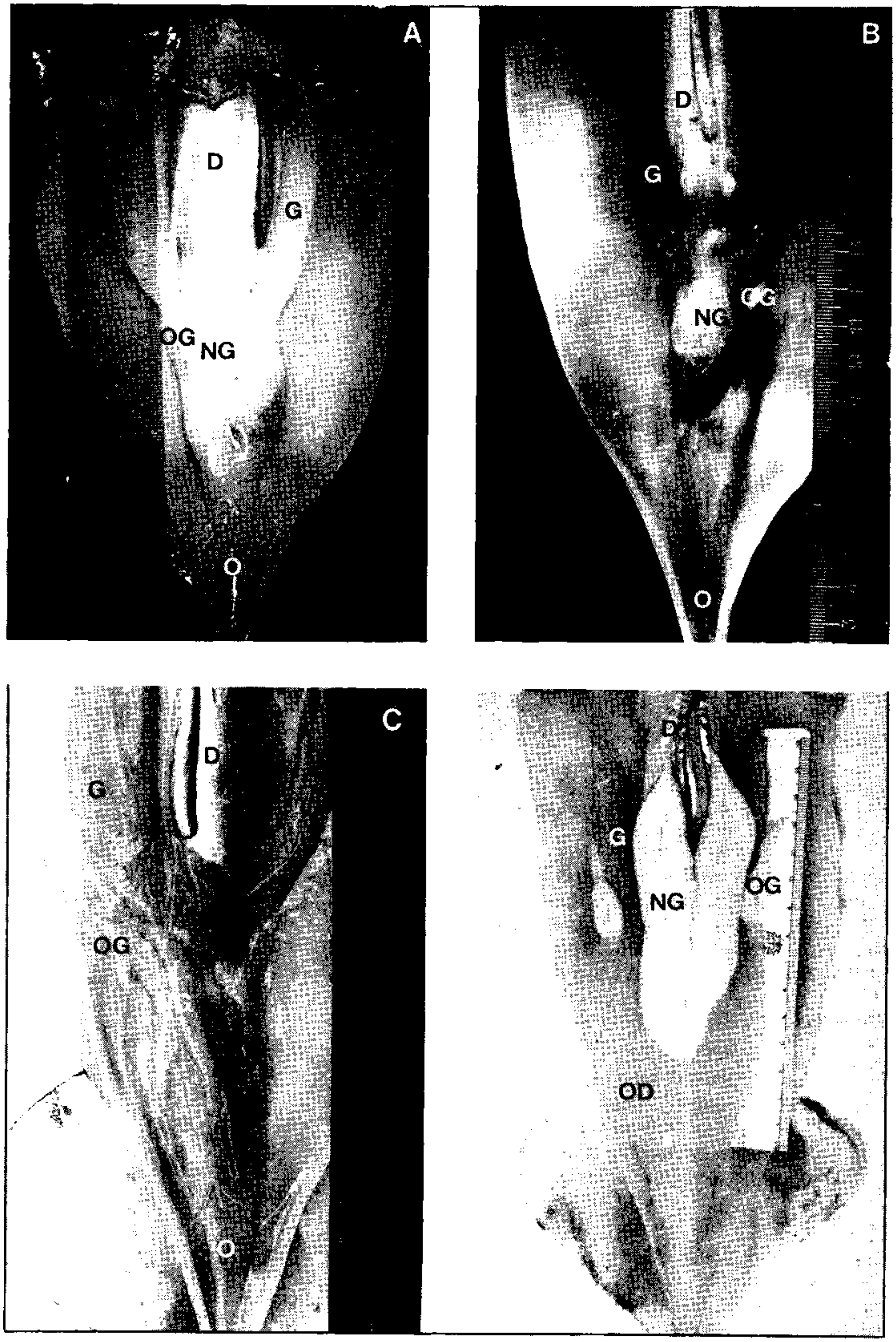

Fig. 5. Typical examples of female *Illex illecebrosus* caught in late spring to early summer(A), summer(B), autumn(C), and early winter from November to January (D). Symbols showing the various organs are the same as those defined in Fig. 2.

Sex determination

The sex is determined by cutting the mantle along the ventral midline and observing the gonads and accessory organs. The general anatomy of each sex is illustrated in Fig. 2 and 3 for females and males respectively. Early in the season (February–June), the key to sexing is the presence of two oviducal glands in the female, one on either side of the stomach, whereas only one gland is present in the male, the spermatophoric gland, located on the animal's left side. Later in the season (July–December), the presence of the two nidamental glands in the mid-ventral area of the female is the key feature for distinguishing the sexes.

Maturity stages

Male. The maturity stages are defined on the basis of Mercer's (MS 1973) criteria, except that his Stage 0 and Stage 1 are combined and listed as Stage 1 below, in order to simplify the assessment of this stage by field observers.

1. *Immature*: spermatophoric organ is thin and transparent to translucent, or with a thin mid-lateral streak; the vas deferens is also thin and transparent or with a slight white streak; the spermatophoric sac is empty.

2. *Maturing;* spermatophoric organ has a white mid-lateral streak; the vas deferens is thick and creamy white in color; the spermatophoric sac may contain a few whitish particles; a representative specimen is shown in Fig. 4A.

3. *Mature:* spermatophoric sac contains spermatophores; the remaining features are the same as for Stage 2; a representative specimen is shown in Fig. 4B.

4. *Spent;* after copulation and release of spermatophores.

Female. The maturity stages are determined from the ratio of the nidamental gland length to mantle length, as defined by Durward *et al.*, (1979). In the field, both the mantle length and nidamental gland length may be measured to the nearest 0.5 cm, although measurements to the nearest millimeter are preferable. The actual maturity stages (Table 1) can be determined later from the field data. Representative females in various stages of development are shown in Fig. 5. Maturing females, resembling those in Fig. 5C and 5D, are very uncommon in field samples, and such specimens should be preserved, whenever possible, for further examination in the laboratory.

TABLE 1. Characteristics of the maturity stages in female *Illex illecebrosus*. (NGL = nidamental gland length, ML = mantle length, and M = limits of NGL/ML defining the maturity stages.)

Maturity stage	Range of NGL (mm)	Range of NGL/ML	Distinguishing features
1	11–25	$M \leqslant 0.09$	NG thin and transparent
2	25–35	$0.09 < M \leqslant 0.125$	NG transparent to translucent ovary grandular
3	25–60	$0.125 < M \leqslant 0.20$	NG translucent to opaque
4	55-90	$0.20 < M \leqslant 0.35$	NG white, oviducts forming
5	110–120	$0.35 < M$	Eggs in oviducts

Source: Durward *et al.* (1979).

Gut fullness

The gut fullness is estimated by visual examination of the stomach (whitish and muscular) and the caecum (thin-walled and translucent) (see Fig. 2) and recorded as *a/b*, where *a* is stomach fullness and *b* is caecum fullness. The numerical scale of fullness is defined as follows: 0 = empty; 1 = half full; 2 = full; and 3 = distended (e.g. 0/1 means that the stomach is empty and the caecum is half full).

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Feeding of Larval Herring, *Clupea harengus*, in the Georges Bank Area, 1965-75[1]

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Abstract

The Georges Bank herring stock is subject to considerable fluctuation due to variable recruitment of year-classes. It is suggested that feeding conditions immediately after hatching is an important factor influencing year-class strength. Annual observations on the feeding of larval herring after mass hatching in October of 1965-75 indicated that only 20% of the larvae examined contained food. Small larvae (5-8 mm) fed mainly on copepod eggs and nauplii and mollusc larvae, whereas the larger larvae fed on the older copepodite stages. The numbers of organisms in the intestines of feeding larvae averaged about two per larvae, which is considerably less than the numbers found in larvae of the North Sea and Baltic Sea. The highest condition factors of larval herring were observed in 1970 and 1971. The very favourable feeding conditions in 1970 probably played an important role in the success of the abundant 1970 year-class of herring on Georges Bank.

Introduction

The herring stock inhabiting Georges Bank (ICNAF Div. 5Z) and adjacent areas is one of the most numerous in the Northwest Atlantic. Its abundance is subject to large fluctuations due to variable year-class recruitment, and hence there has been marked variation in yield. For example, the nominal catches of herring in Subarea 5 and Statistical Area 6 declined from more than 220,000 tons in 1962 to 76,000 tons in 1965, increased rapidly to 436,000 tons in 1968 and then gradually declined to 94,000 tons in 1976 of which less than half were taken in the offshore fishery. One of the primary factors determining the strength of year-classes in the majority of fish species is considered to be the feeding conditions during the very early stages of larval development. Beginning in 1965, USSR scientists from AtlantNIRO initiated studies on distribution, abundance, composition and feeding intensity of larval herring in the Georges Bank area, as well as studies on the composition and abundance of zooplankton. This paper presents the results of studies on the feeding of larval herring during 1965-75.

Materials and Methods

Ichthyoplankton surveys on the abundance and distribution of larval herring on Georges Bank and in adjacent waters of the Gulf of Maine were conducted in October of each year after the hatching of larvae occurred on the main spawning grounds. In the period of 1965-70, the surveys were made according to the pattern of stations shown in Fig. 1A, using a conical plankton net with opening diameter of 80 cm and mesh size of 0.570 mm. At each station, a vertical haul was made from 50 m to the surface and a haul near the surface for a duration of 10-15 minutes. All stations were usually occupied except in 1970 when the ichthyoplankton samples were collected over the spawning ground on the northern part of Georges Bank. From 1971 to 1975 the surveys were conducted under the International Larval Herring Survey Program coordinated by ICNAF and following the pattern of stations shown in Fig. 1B. Plankton hauls were made using a BONGO sampler with opening diameter of 61 cm and mesh sizes of 0.333 and 0.505 mm. Each haul of 15 minutes duration at a vessel speed of 3.5 knots was made by depth level from 100 m to the surface. The ichthyoplankton samples were preserved in 4% formalin for subsequent laboratory examination.

Analysis of the diurnal feeding habits of larval herring indicated that they do not feed at night (Fig. 2). Therefore, only the samples taken during daylight hours were selected for the feeding studies. The methods described by Bokova (1961) were used in processing the data. The herring larvae were measured (mm) from the tip of the snout to the posterior end of the notochord. Mean weights of larvae were determined by grouping not more than 10 specimens of the same body length on filtering paper to dry for about 1 minute and then weighing the group on an analytical balance. The larvae were then dissected and

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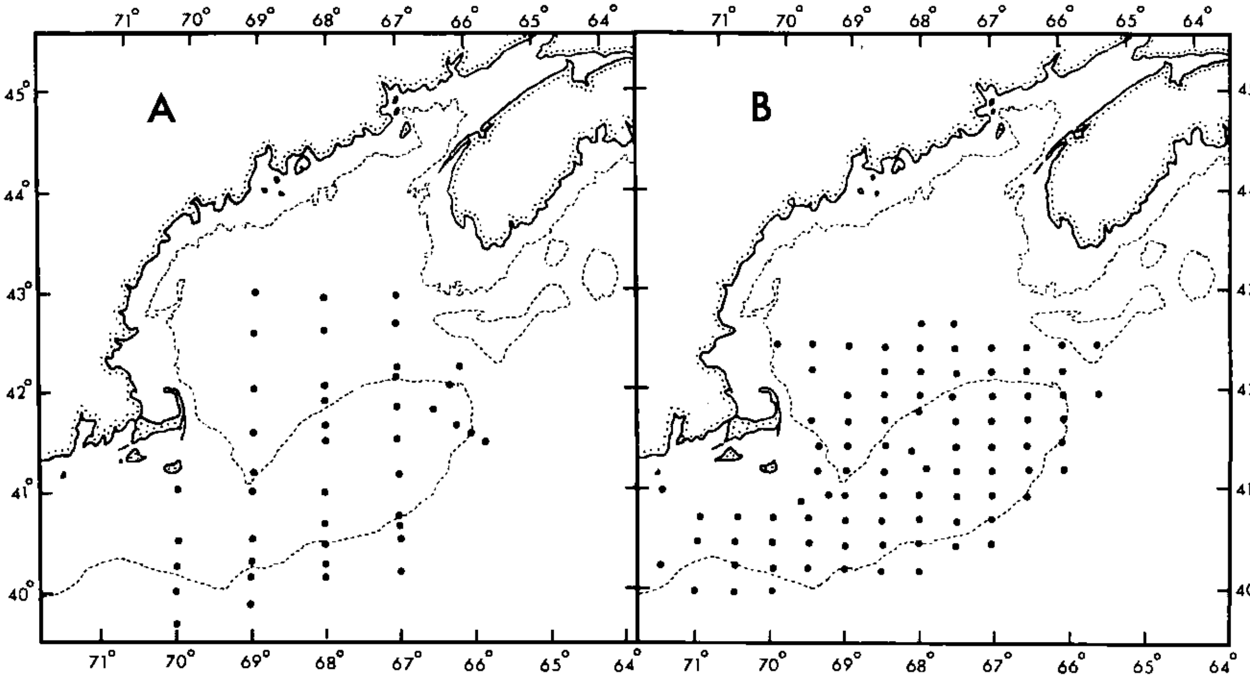

Fig. 1. Ichthyoplankton survey stations in the Georges Bank area from which material was collected for feeding studies in larval herring. A. Stations used in 1965–70. B. Stations used in 1971–75.

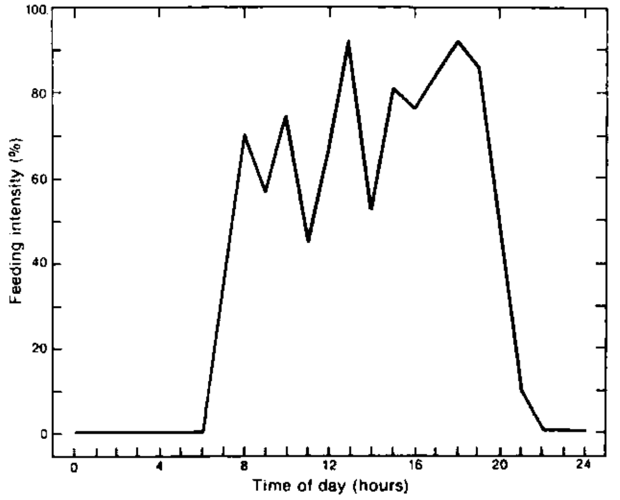

Fig. 2. Diurnal pattern of the feeding intensity of larval herring on Georges Bank in October 1972.

the food organisms in the intestines were classified by genera where possible. The smaller organisms were assigned to groups such as copepod eggs, copepod nauplii, mollusc larvae, etc. Heavily digested organisms were identified at the level of Order. All food organisms were measured and their degree of digestion recorded using the following scale: (1) whole fresh organisms, (2) partly digested organisms, (3) digested organisms except for carapace, and (4) completely digested organisms (some non-assimilated parts of the body). On the basis of information relating the body length of the organisms to weight (Bogarov and Preobrazhenskaya, 1934; Kanaeva, 1962; Shmeleva, 1963), the weights of the different food organisms were determined from the actual measurements of whole organisms. Mean weights of the groups of whole organisms were used to estimate the weights of heavily digested food organisms. For analysis, all of the results were combined for three size groups of herring larvae as follows:

a) 5.0–7.9 mm — larvae having yolk-sacs, but already consuming small food organisms;
b) 8.0–12.9 mm — larvae feeding mainly on small organisms (copepod eggs and nauplii);
c) 13.0–17.9 mm — larvae feeding mainly on copepodites.

The feeding intensity was estimated as the proportion of herring larvae containing food and the feeding index for each length group was taken as the ratio of the mean weight of food organisms to the weight of larvae containing food. To evaluate year-to-year variation in the condition factor of the larvae, weights of larvae by length group and year were compared with mean weights for the series of observations (Noskov, 1956).

In addition to the ichthyoplankton samples, zooplankton samples were collected with a Juday plankton net in 1965-70 and with a small-meshed net in the BONGO sampler during 1971-75.

Results and Discussion

During the period of observation in the Georges Bank area, the feeding intensity of larval herring ranged from a low of 3% in 1966 to 66% in 1972, the average being 21% of nearly 4,000 larvae examined in 1965-75 (Table 1). The overall feeding intensity of 8.0-12.9 mm larvae (28%) was only slightly less than that for the 13.0-17.9 mm larvae (33%) but was considerably lower (11%) for the small larvae of 5.0-7.9 mm. This latter result can be attributed to lower feeding intensity during yolk-sac resorption. In general, the average feeding intensity of larval herring in the Georges Bank area is lower than that reported for gulfs and bays where zooplankton food is abundant. According to Lebour (1921), Bhattacharyya (1957) and Schnack (1972), about 30, 45 and 50% respectively of the larval herring from the North Sea contained food. Sherman and Honey (1968) reported that 43% of the larval herring examined from the Gulf of Maine contained food, Pokrovskaya (1955) found food in 44% of the intestines of Pacific larval herring, and Schnack (1972) found food in all larval herring from the western Baltic (Schley Fjord) except in a few very small specimens.

As indicated by Samyshev and Ptitsina (1976) the transition to active feeding for larval herring on Georges Bank begins upon attaining a length of about 5 mm. The basic food components at first are mostly small organisms such as copepod eggs and nauplii and mollusc larvae (Tables 2 and 3). In the 8.0-12.9 mm larvae, the smaller copepodite stages of *Oithona* spp., *Centropages* spp. and *Paracalanus* spp. become more prevalent in the diet. The larger larvae of 13.0-17.9 mm in length feed mainly on larger copepodite stages of *Paracalanus* spp., *Pseudocalanus* spp. and *Calanus finmarchicus*. Although 28 taxonomic groups were represented in the food of the larval herring, only nine groups covering a wide range of prey size were predominant, and it is clear that the smaller the larvae, the smaller the food organisms consumed.

The number of food organisms per feeding larave in the Georges Bank area during 1965-75 is considered to be low (Table 4), averaging 1.6, 2.4 and 2.0 in the small-, medium- and large-sized larvae respectively, and the feeding index varied greatly from year-to-year, averaging 0.30, 0.21 and 0.07 respectively. Thus, a declining trend in the feeding index with growth is evident. The highest feeding index values for small larvae occur in 1965, 1969 and 1973, for medium-size larvae in 1968, 1969 and 1973, and for large larvae in 1969, 1970 and 1973. Judging by the number of food organisms per feeding larvae, larval herring on Georges Bank feed less intensively than in the North Sea where a feeding larvae contains an average of 4 food organisms and in Schley Fjord where larvae of 14 and 19 mm contain 4.5 and 8.2 organisms each respectively.

Analysis of zooplankton samples from Georges Bank in 1965-75 indicates that the total abundance of food organisms in October varied greatly from year-to-year with *Oithona* spp., *Centropages* spp. and copepod nauplii predominating (Table 5). The high abundance of food zooplankton recorded in 1969 and 1970 was due to a sharp increase in the abundance of *Oithona* spp. These years were evidently characterized by better feeding conditions for herring larvae in October than in the other years. From studies on herring in the Baltic Sea, Lisivnenko (1960, 1961) showed a positive correlation betwen the abundance of zooplankton and the strength of herring year-

TABLE 1. Numbers of larval herring examined by size groups and percentages containing food from ichthyoplankton surveys in the Georges Bank area, 1965-75. (See "Materials and Methods" for description of gear and methods used during 1965-70 and 1971-75.)

Year	Dates of survey	5.0-7.9 mm		8.0-12.9 mm		13.0-17.9 mm		Total	
		No. of larvae	% with food	No. of larvae	% with food	No. of larvae	% with food	No. of larvae	% with food
1965	8-11 Oct	521	14.8	77	29.9	15	26.7	613	17.0
1966	7-14 Oct	307	1.3	60	10.0	0	0.0	367	2.7
1968	6-9 Oct	72	0.0	154	22.7	31	19.4	257	15.9
1969	11-16 Oct	101	21.8	66	27.3	65	41.5	232	28.9
1970	14-28 Oct	200	1.5	93	26.9	17	29.4	310	10.6
1971	9-25 Oct	42	11.9	136	35.3	211	28.0	389	28.8
1972	13-28 Oct	28	50.0	68	73.5	32	65.6	128	66.4
1973	15 Oct-1 Nov	162	8.0	116	43.1	219	38.8	497	29.8
1974	18-30 Oct	226	20.4	336	23.8	112	37.5	674	24.9
1975	17-30 Oct	164	12.2	297	19.5	57	3.5	518	15.4
Totals		1,823	11.2	1,403	28.0	759	33.1	3,985	21.3

TABLE 2. Frequency of occurrence (%) of food items in three length groups of larval herring from the Georges Bank area, 1965-75.

Larvae length (mm)	Food items	Size of prey (mm)	Occurrence frequency of food items										Average frequency 1965-75
			1965	1966	1968	1969	1970	1971	1972	1973	1974	1975	
5.0–7.9	Mollusc larvae	0.10–0.20	48	—	—	45	—	—	—	8	2	5	24
	Copepod eggs	0.10–0.13	1	—	—	9	50	—	—	15	22	25	10
	Copepod nauplii	0.18–0.32	65	100	—	14	—	100	100	62	70	85	65
	Centropages spp.	0.40	—	—	—	—	—	—	—	—	4	—	1
	Oithona spp.	0.50–0.65	8	—	—	14	—	—	—	15	4	—	6
	Paracalanus spp.	—	—	—	—	—	—	—	—	—	—	—	—
	Pseudocalanus spp.	—	—	—	—	—	—	—	—	—	—	—	—
	Calanus finmarchicus	1.40	1	—	—	—	—	—	—	—	—	—	+
	Other food items[a]	0.40–0.75	9	—	—	41	50	—	—	8	4	10	11
	No. of feeding larvae		**77**	**4**	**—**	**22**	**3**	**5**	**14**	**13**	**46**	**20**	**204**
8.0–12.9	Mollusc larvae	0.15–0.22	6	—	43	33	8	4	—	2	1	—	7
	Copepod eggs	0.15–0.25	4	—	—	—	—	—	—	—	14	3	4
	Copepod nauplii	0.20–0.33	83	67	—	17	25	48	80	30	48	43	44
	Centropages spp.	0.40–0.70	—	—	11	—	—	10	26	12	2	2	8
	Oithona spp.	0.50–0.70	22	—	3	11	25	12	6	34	20	50	22
	Paracalanus spp.	0.70–0.90	—	—	3	—	—	4	—	40	1	3	6
	Pseudocalanus spp.	0.80–1.00	—	—	—	—	—	8	—	2	1	—	1
	Calanus finmarchicus	1.00	26	—	—	—	—	—	—	—	—	—	2
	Other food items[a]	0.48–1.10	9	67	54	89	75	64	38	48	41	33	47
	No. of feeding larvae		**23**	**6**	**35**	**18**	**25**	**48**	**50**	**50**	**80**	**58**	**393**
13.0–17.9	Mollusc larvae	0.21	—	—	—	15	—	—	—	—	—	—	2
	Copepod eggs	0.10–0.20	—	—	—	—	—	—	5	2	2	—	1
	Copepod nauplii	0.21–0.40	25	—	—	7	—	17	28	1	17	—	11
	Centropages spp.	0.57–0.70	—	—	17	—	—	3	10	13	—	—	6
	Oithona spp.	0.60–0.78	—	—	—	4	—	3	33	18	36	100	17
	Paracalanus spp.	0.84–0.92	—	—	—	26	50	41	10	41	19	—	31
	Pseudocalanus spp.	0.95–1.25	—	—	—	—	—	12	14	14	—	—	9
	Calanus finmarchicus	1.00–1.50	75	—	—	—	—	—	5	—	—	—	2
	Other food items[a]	0.66–1.15	—	—	100	74	50	59	57	36	45	—	50
	No. of feeding larvae		**4**	**—**	**6**	**27**	**5**	**59**	**21**	**85**	**42**	**2**	**251**

[a] Copepods and digested food.

TABLE 3. Percentage composition by weight of food items in three length groups of larval herring from the Georges Bank area, 1965–75.

Larvae length (mm)	Food items	Size of prey (mm)	Percentage food composition by weight										Weighted average 1965–75
			1965	1966	1968	1969	1970	1971	1972	1973	1974	1975	
5.0–7.9	Mollusc larvae	0.10–0.20	69	—	—	86	—	—	—	48	12	24	43
	Copepod eggs	0.10–0.13	+	—	—	2	50	—	—	3	12	11	5
	Copepod nauplii	0.18–0.32	21	100	—	2	—	100	100	35	41	54	36
	Centropages spp.	0.40	—	—	—	—	—	—	—	—	8	—	1
	Oithona spp.	0.50–0.85	2	—	—	4	—	—	—	6	4	—	2
	Paracalanus spp.	—	—	—	—	—	—	—	—	—	—	—	—
	Pseudocalanus spp.	—	—	—	—	—	—	—	—	—	—	—	—
	Calanus finmarchicus	1.40	8	—	—	—	—	—	—	—	—	—	3
	Other food items[a]	0.40–0.75	+	—	—	6	50	—	—	8	25	11	10
	No. of feeding larvae		**77**	**4**	**—**	**22**	**3**	**5**	**14**	**13**	**46**	**20**	**204**
8.0–12.9	Mollusc larvae	0.15–0.22	28	—	46	45	29	7	—	2	2	—	11
	Copepod eggs	0.15–0.25	2	—	—	—	—	—	—	—	1	1	+
	Copepod nauplii	0.20–0.33	43	37	—	1	5	16	42	5	10	17	16
	Centropages spp.	0.40–0.70	—	—	11	—	—	10	30	14	2	2	9
	Oithona spp.	0.50–0.70	6	—	2	4	13	7	6	15	9	29	11
	Paracalanus spp.	0.70–0.90	—	—	6	—	—	13	—	6	4	7	5
	Pseudocalanus spp.	0.80–1.00	—	—	—	—	—	9	—	4	6	—	3
	Calanus finmarchicus	1.00	20	—	—	—	—	—	—	—	—	—	1
	Other food items[a]	0.48–1.10	1	63	35	50	53	38	22	54	66	44	44
	No. of feeding larvae		**23**	**6**	**35**	**18**	**25**	**48**	**50**	**50**	**80**	**58**	**393**
13.0–17.9	Mollusc larvae	0.21	—	—	—	8	—	—	—	—	—	—	1
	Copepod eggs	0.10–0.20	—	—	—	—	—	—	+	+	+	—	+
	Copepod nauplii	0.21–0.40	22	—	—	1	—	2	3	+	2	—	2
	Centropages spp.	0.57–0.70	—	—	5	—	—	1	4	9	—	—	4
	Oithona spp.	0.60–0.78	—	—	—	+	—	+	5	3	15	100	5
	Paracalanus spp.	0.84–0.92	—	—	—	43	50	46	4	39	38	—	36
	Pseudocalanus spp.	0.95–1.25	—	—	—	—	—	14	10	25	—	—	13
	Calanus finmarchicus	1.00–1.50	78	—	—	—	—	—	42	—	—	—	5
	Other food items[a]	0.66–1.15	—	—	95	48	50	36	32	24	45	—	34
	No. of feeding larvae		**4**	**—**	**6**	**27**	**5**	**59**	**21**	**85**	**42**	**2**	**251**

[a] Copepods and digested food.

TABLE 4. Number of organisms consumed per feeding larvae and and the feeding index by size group for larval herring in the Georges Bank area, 1965–75.

	5.0–7.9 mm		8.0–12.9 mm		13.0–17.9 mm	
Year	Number of organisms	Feeding index	Number of organisms	Feeding index	Number of organisms	Feeding index
1965	2.0	0.834	2.6	0.162	1.2	0.015
1966	1.0	0.120	4.0	0.101	—	—
1968	—	—	1.7	0.440	1.8	0.093
1969	1.5	0.380	2.0	0.367	2.6	0.117
1970	1.3	0.094	2.0	0.153	1.5	0.107
1971	2.4	0.136	2.8	0.145	2.4	0.067
1972	1.3	0.116	3.3	0.166	2.8	0.073
1973	2.6	0.567	2.0	0.222	2.4	0.088
1974	1.4	0.178	1.5	0.172	1.4	0.057
1975	2.2	0.279	1.9	0.138	1.5	0.031
1965–75	1.6	0.300	2.4	0.207	2.0	0.072

TABLE 5. Number of organisms per liter of water in zooplankton hauls on Georges Bank, 1965–75.

Food organisms	Size (mm)	1965	1966	1966	1969	1970	1972	1973	1975
Copepod eggs, nauplii	0.1–0.5	0.69	0.74	0.28	1.29	1.75	0.05	0.28	4.70
Oithona spp.	0.2–1.2	2.61	5.12	2.94	13.12	9.37	2.83	6.21	1.39
Paracalanus spp.	0.2–1.2	0.01	0.02	0.06	0.17	0.28	0.21	0.33	1.34
Centropages spp.	0.2–1.4	0.20	0.38	1.00	0.61	1.44	2.50	2.35	0.86
Pseudocalanus spp.	0.2–1.5	0.24	0.08	0.44	0.49	0.33	0.23	0.73	0.22
Total		3.75	6.34	4.72	15.68	13.17	5.82	9.90	8.51

classes. It is therefore likely that the relatively strong 1970 year-class of herring on Georges Bank resulted from better survival of the larvae due to the higher-than-average abundance of food zooplankton. Schnack (1972) estimated that the optimum abundance of food organisms for the feeding of larval herring should be about 200 specimens per liter. However, the abundance in October on Georges Bank fluctuated between 4 and 16 specimens during 1965–75.

The condition factor of larval herring may be taken as a summed index of feeding conditions, the availability and quality of the food being its main components. As an indication of year-to-year variation in the condition factor, the divergence of the mean weights of larvae by length for each year from the long-term mean values are given in Table 6. The condition factor was observed to be highest in 1970 and 1971, in which the weight of 10 mm larvae was 28% higher than the average for the period as a whole. After 1966, the only abundant year-class of herring was that of 1970, and it is suggested that the better-than-average condition of the larval herring in October 1970 promoted higher survival. Such cannot be said for the very poor 1971 year-class, indicating that a multiplicity of factors must affect year-class strength including environmental conditions throughout the winter following hatching in the autumn.

Summary

The herring stocks in the Georges Bank area are subject to considerable fluctuations due to great variation in recruitment of year-classes. The availability of food during and immediately following the stage of yolk-sac resorption is considered to be one of the primary factors affecting year-class strength.

This study of the feeding habits of larval herring and the availability of food is based on ichthyoplankton and zooplankton samples collected annually in October during 1965–75. Only about 20% of the herring larvae (5–18 mm in length) examined had food in their intestines, and the results show that the smaller larvae (<8 mm) fed less intensively than the larger ones. The food of the smaller larvae consisted mostly of copepod eggs and nauplii and sometimes mollusc larvae, whereas the larger larvae fed mainly on the larger copepodite stages.

The mean numbers of organisms found in the intestines of the small-, medium- and large-sized larvae were 1.6, 2.4 and 2.0 respectively, indicating that the feeding of larval herring on Georges Bank was less intensive on the average than in other regions, especially if compared with conditions in the North Sea and in Schley Fjord in the western part of the Baltic

TABLE 6. Mean weight (mg) by length and divergence of mean weights from 1966–75 averages for larval herring in the Georges Bank area.

Length (mm)	Years of surveys 1966	1968	1969	1970	1971	1972	1973	1974	1975	Average 1966–75
					Mean weights of larvae (mg)					
5	0.10	—	—	—	—	—	—	—	—	0.10
6	0.13	0.17	—	0.27	—	—	0.16	0.18	0.16	0.18
7	0.17	0.24	0.31	0.35	0.34	0.29	0.25	0.28	0.22	0.27
8	—	0.32	0.40	0.48	0.54	0.42	0.40	0.38	0.32	0.41
9	—	0.41	0.55	0.68	0.80	0.63	0.60	0.55	0.51	0.59
10	—	0.52	0.71	1.05	1.05	0.90	0.81	0.75	0.80	0.82
11	—	0.64	0.90	—	1.41	1.18	1.20	1.00	1.06	1.06
12	—	0.76	—	—	2.05	2.00	1.80	1.20	1.40	1.54
13	—	—	—	—	2.50	2.50	2.20	1.80	1.85	2.17
14	—	—	—	—	3.30	3.10	2.90	2.60	2.50	2.88
15	—	—	—	—	4.50	3.80	3.90	3.60	3.20	3.80
16	—	—	—	—	6.50	5.00	5.10	5.00	4.30	5.18
17	—	—	—	—	9.50	6.70	8.70	6.75	—	7.41
					Divergence of mean weights from 1966–75 average (%)					
5	100	—	—	—	—	—	—	—	—	100
6	72	94	—	150	—	—	89	100	89	100
7	63	89	115	130	126	107	93	96	82	100
8	—	78	98	117	132	102	98	93	78	100
9	—	70	93	115	136	107	102	93	86	100
10	—	63	87	128	128	110	98	91	98	100
11	—	60	85	—	133	111	113	94	100	100
12	—	49	—	—	133	129	117	78	91	100
13	—	—	—	—	115	115	101	83	85	100
14	—	—	—	—	115	108	101	90	87	100
15	—	—	—	—	118	100	103	95	84	100
16	—	—	—	—	126	97	98	97	83	100
17	—	—	—	—	128	90	90	91	—	100

where feeding larvae contained an average of four or more organisms each.

The highest condition factors were recorded in 1970 and 1971. Since the 1970 year-class of herring was the most numerous in the period under study, it is suggested that the favourable feeding conditions in that year enhanced the survival of the larvae. However, it should be noted that year-class strength is affected by conditions not only immediately after hatching in the autumn but also during the winter up to the time of zooplankton development in the spring.

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Current Mesh Selection Studies on the Scotian Shelf in Relation to Historical Selectivity Data[1]

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Abstract

Mesh selection data for haddock, cod, pollock, red hake, silver hake, redfish, American plaice, witch flounder, alewife and mackerel.collected during joint Canada-Cuba and Canada-USSR cruises on the Scotian Shelf in 1977, are compared with general selection patterns for these species based on historical selectivity data. Most of the 50% retention lengths for the various groundfish species sampled fit the historical selection patterns reasonably well. Since a certain amount of variability is generally inherent in mesh selection studies, such a selection pattern for a species could be considered as a "commercial average" and utilized in analyzing the effects of mesh regulations. This raises the question of the necessity for further mesh selection studies on species for which much data already exist.

Introduction

The results of mesh selection studies for various finfish species (cod, haddock, redfish, pollock, red hake, silver hake, American plaice, witch flounder, alewife and mackerel) presented in this paper are based on data collected in the summer and autumn of 1977 during joint Canada-Cuba and Canada-USSR cruises. Although these cruises were originated to study the mesh selection of silver hake, *Merluccius bilinearis*, a valuable offshoot has been information on the selection of other species. There is a lack of information on small mesh kapron codend selectivity of the Scotian Shelf (kapron is a polyamide synthetic material of trawls used extensively by the Cuban and USSR fishing fleets).

Measures agreed upon for the silver hake fishery on the Scotian Shelf limit the codend mesh size of mid-water trawls to a minimum of 60 mm (ICNAF, 1977a). An area restriction for bottom trawls limits the codend mesh size to 60 mm seaward of the "small mesh gear line" (ICNAF, 1977b) (Fig. l). The aims of these regulations were to increase the maximum sustainable yield of the silver hake fishery and, possibly, to reduce the undesirable by-catch of juveniles of other commercially important species. The purpose of the two joint mesh selection studies undertaken in 1977 was to quantify the effects of these new measures upon the silver hake fishery. The results of the studies pertaining to silver hake have been documented by Clay (MS 1978).

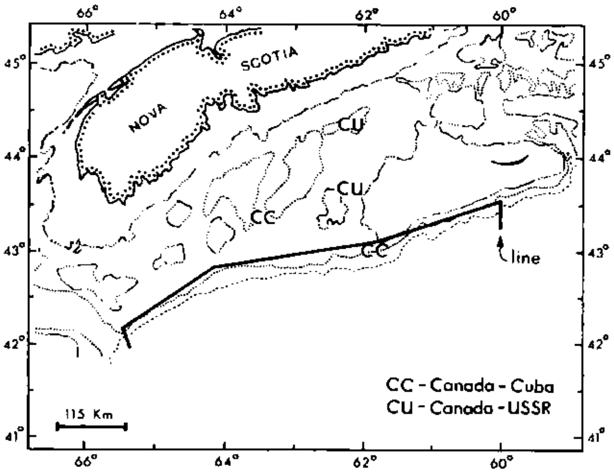

Fig. 1. Map showing the "small mesh gear line" and the approximate locations of the joint Canada-Cuba and Canada-USSR mesh selection studies in 1977.

Methods

The specifications of the research vessels and the gears used are listed in Table 1. On the USSR R/V *Foton*, a topside cover was fitted to the codend in a manner similar to the ICES specifications (ICES, 1964). The general construction and dimensions of the cover are shown in Fig. 2. On the Cuban R/V *Isla de la Juventud*, exact details of the attachment of the cover are not available in the cruise reports, although Hare

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TABLE 1. Specifications of research vessels and gears used in the joint mesh selection studies in 1977.

	Cuba	USSR
	R/V *Isla de la Juventud*	R/V *Foton*
Overall length (m)	70.3	54.6
Beam (m)	12.5	.....
Displacement — net (tons)	1,556	660
— gross (tons)	2,200	987
Engine power (HP)	2,400	800
Speed (knots)	14.5	10
Type of vessel	Stern trawler (freezer)	Side trawler
Type of trawl	Bottom trawl[a]	Bottom trawl
Footrope length (m)	57.9	31.4
Headrope length (m)	41.6	28.0
Headrope height (m)	6.0	5.0
Wing spread (m)	unknown	11.0
Length of bridles (m)	113	50
Type of doors	oval	oval steel
Weight of door (kg)	1,500	650
Area of door (m^2)	5.5	(2.75 × 1.80)
Mesh size of wings (mm)	204	200
Mesh size — square (mm)	200	
— middle (mm)	150	160
— end (mm)	123	
Mesh size of codend (mm)	(1) 40.1[b]	(1) 39.6
	(2) 66.1[b]	(2) 59.8
	(3) 90.2[b]	(3) 69.7
		(4) 124.1
Liner in codend	yes[c]	no
Cover on codend	yes	yes
Mesh size of cover (mm)	20	34.5
Chafing gear fitted	yes	no
Rollers on footrope	no	yes[d]
Codend material	kapron	kapron
Codend twine	unknown	93.5 tex × 18[e]
Cover material	kapron	kapron
Cover twine	unknown	93.5 tex × 12

[a] Spanish type.

[b] Same measurements for wet and dry codends.

[c] Liner covering the codend knot.

[d] Steel rollers, 145 mm diameter, were connected through their centers with a heavy cable, and the entire apparatus was connected to the footrope by chains 18 cm long.

[e] Twine assumed to be 93.5 tex × 12 for 124.1 mm codend.

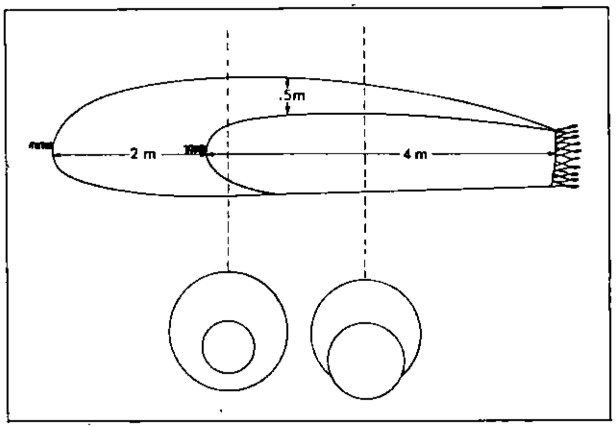

Fig. 2. Schematic diagram and dimensions of the topside covered codend used by the USSR R/V *Foton* during the joint Canada-USSR mesh selection study in 1977.

(personal communication) recalls that the cover was attached close to the codend. This would probably depress the 50% retention length and reduce the selection range (Clay, MS 1978).

TABLE 2. Results of mesh measurements of codends and covers used on Cuban and USSR reseach vessels during joint mesh selection studies on the Scotian Shelf in 1977.

Commercial rated mesh size (mm)	Measured wet		Measured dry	
	No. of meshes	Mean ± SD (mm)	No. of meshes	Mean ± SD (mm)
	R/V *Isla de la Juventud* (Cuba)			
20[a]		20.1		20.0
50		40.1		40.1
60		66.1		66.1
90		90.2		90.0
	R/V *Foton* (USSR)			
30[a]	10	34.5 ± 1.5	10	32.6 ± 1.3
40	10	39.6 ± 1.5	10	33.4 ± 1.5
60	30	59.8 ± 1.5	10	56.4 ± 1.3
70	30	69.7 ± 1.7	10	65.8 ± 2.1
120	20	124.1 ± 3.1	—	— —

[a] Measurements small-meshed cover.

Codend mesh sizes (Table 2) were determined by measuring the stretched mesh with an ICNAF gauge at 4 kg pressure. The codend mesh sizes used throughout the paper refer to the designated commercial mesh sizes. The fish were measured as total length to the nearest centimeter. The locations of the study areas are indicated in Fig. 1.

The data collected during these series of covered codend mesh selection experiments were analyzed according to the methods suggested by Pope *et al.* (1964, 1975) and Holden (1971). These authors indicate that fitting the selection ogive by the maximum likelihood method is the most accurate means of deriving the curve. However, the tedious calculations associated with this method are not often warranted, as it has been found that fitting the curves by eye give unbiased estimates (Pope *et al.* 1964) which are very close (often within 1%) to those obtained by the maximum likelihood method (Holden, 1971). After comparing several methods in studying selection of silver hake (Clay, MS 1978), it was decided to estimate the 50% retention lengths from curves fitted by eye to the present data. A "general selection pattern" was estimated for each species, for which adequate historical data were available, by calculating a geometric mean regression (Ricker, 1975) of 50% retention length against stretched mesh size, and the results of the 1977 studies were compared with the general patterns.

Results

The results of the cooperative mesh selection studies in 1977 for various groundfish species have been compared with historical data reported by Holden (1971). In most cases, the present results appear to fit within the historical patterns. For some species, past studies indicate rather high correlations between 50% retention lengths and codend mesh sizes despite great variation in trawl materials used, in the types of gauges used in mesh measuring, in the speed and duration of tow and in the size of catch. Some of these earlier studies used polyamide materials in the codends, this type of material is the closest to kapron for which comparative data are available. The actual type of material used in net construction may not be an important factor, as according to Holden (1971), it was "not possible to demonstrate any relationship between selectivity and the physical properties of the net materials".

Haddock, *Melanogrammus aeglefinus*

Selection curves for haddock from the cooperative studies in 1977 are shown in Fig. 3. Fifty percent retention lengths of 190, 210, 230, 340 and 480 mm were estimated for covered codends hauls by trawls with codend meshes of 60, 60, 70, 90, and 120 mm respectively. These five points are indicated by triangles on the scatter diagram of historical selectivity data (Fig. 4), for which the general selection pattern was calculated to be

$$TL = 3.63\ M - 28.49 \qquad (r^2 = 0.85,\ n = 296)$$

where TL is the 50% retention length of haddock (total

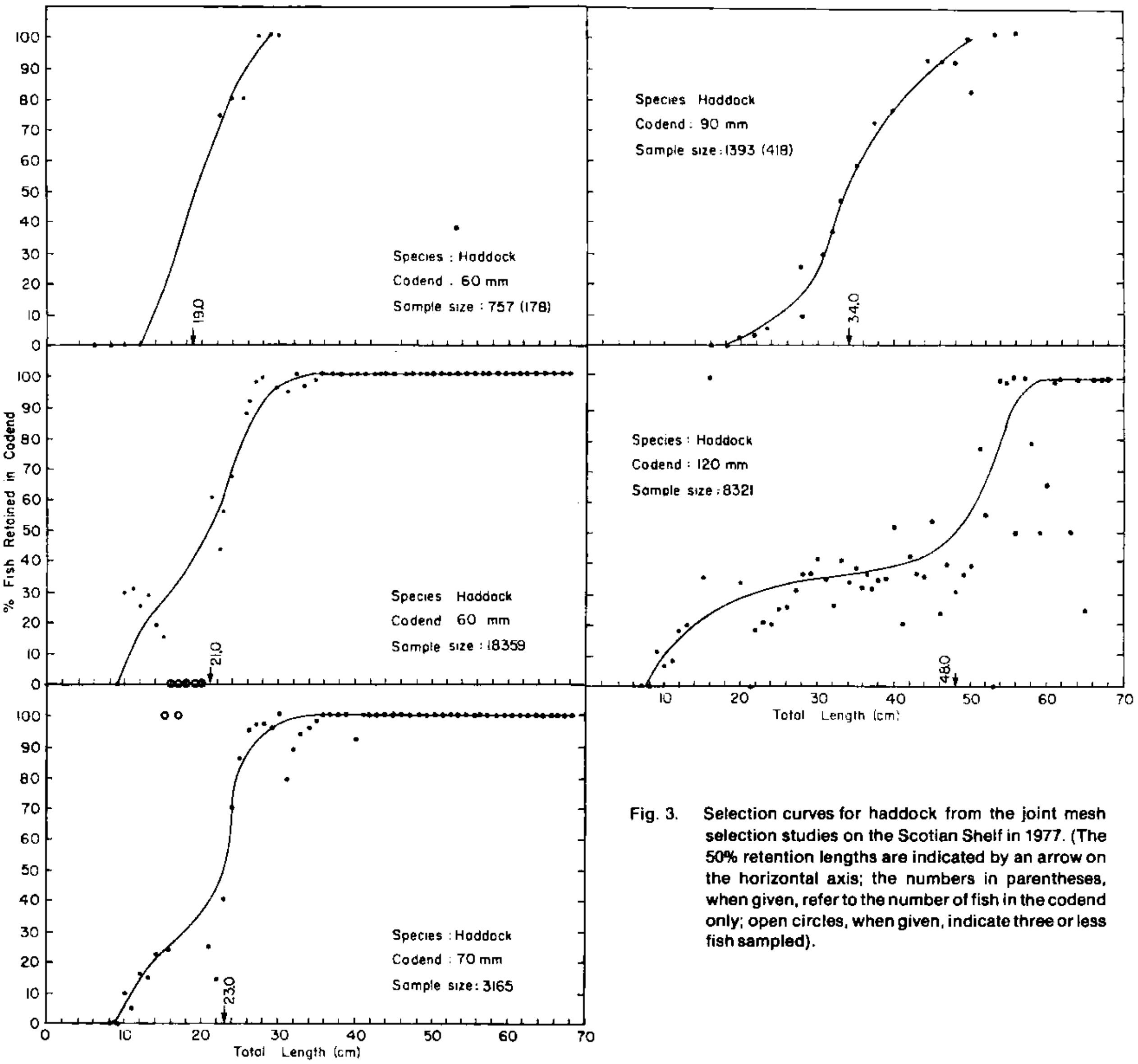

Fig. 3. Selection curves for haddock from the joint mesh selection studies on the Scotian Shelf in 1977. (The 50% retention lengths are indicated by an arrow on the horizontal axis; the numbers in parentheses, when given, refer to the number of fish in the codend only; open circles, when given, indicate three or less fish sampled).

length in mm), and M is the codend mesh size (mm). Also shown in Fig. 4 is an approximation to the length-girth relationships for haddock as reported by Wells (1969)[1] for the Newfoundland area and by Margetts (1954) for the North Sea. The relationship (dashed line) is defined by G = 0.55 TL - 1.5, where the girth (G) is expressed in centimeters. Throughout this paper the girth is assumed to be equal to twice the stretched mesh. The results from the 1977 studies for the 60 mm and 70 mm mesh codends are consistent with the historical data (Fig. 4), but the 50% retention lengths for the 90 mm and 120 mm mesh codends are above the regression line, indicating the escapement of larger fish than would be expected. However, the regression line can give a reasonably good estimate of the 50% retention length for any mesh size within the range of the experiments, and, considering the variability in the results of mesh selection studies, the estimate for a particular mesh size is probably close to the commercial average for fishing operations.

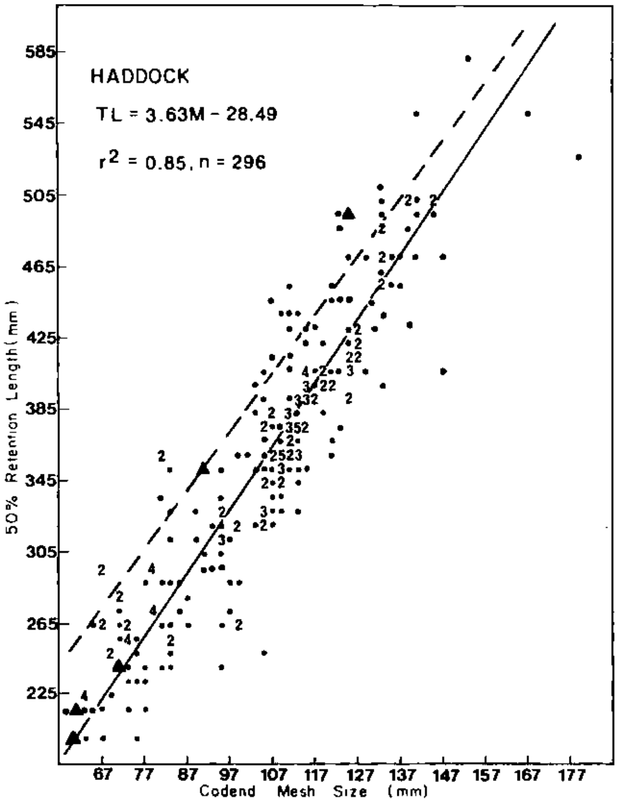

Fig. 4. General selection pattern for haddock based on historical mesh selection studies. (Each dot represents a single observation and numbers indicate points with two or more observations; triangles indicate points from the 1977 studies; the dashed line represents the length-girth relationship. The scatter graphs used throughout this paper are computer plots and as such have lower resolution than was found in the original data.)

Atlantic cod, *Gadus morhua*

Insufficient data for cod were collected during the Canada-USSR mesh selection studies to allow the construction of any selection curves and only the curve for the 90 mm mesh with a 50% retention length of 385 mm was estimated from data collected during the Canada-Cuba studies (Fig. 5). An analysis of historical selectivity data gave the general selection pattern (Fig. 6) defined by the regression

$$TL = 4.35\ M - 87.62 \qquad (r^2 = 0.51,\ n = 198)$$

and two length-girth relationships based on data reported separately in several references. The first, labelled "Girth 1" in Fig. 6, is approximately G = 0.50 TL =0.75, based on relationships reported by Hodder and May (1965)[1], Cendrero (MS 1965)[1] and Bohl (1966a, 1967), and the second, labelled "Girth 2", is approximately G = 0.56 TL - 1.50, based on relationships reported by Hodder and May (1965)[1], Wiles and May (1968)[1], Bohl (MS 1966b) and Cendrero (MS 1965)[1]. Both length-girth relationships include data from different geographical regions of the Northwest Atlantic and for different periods of the year although no trend was noted. The 50% retention length for the 90 mm mesh from the Canada-Cuba study is well above the regression line (Fig. 6), again indicating the escapement of larger fish than would be expected.

Other gadoids

Examination of available data for other gadoid species collected during the 1977 cooperative studies reveal that the 50% retention length for pollock, *Pollachius virens*, with a 90 mm mesh is 380 mm (Fig. 7), which is virtually the same as that obtained for cod (see Fig. 5). The 50% retention lengths for red hake,

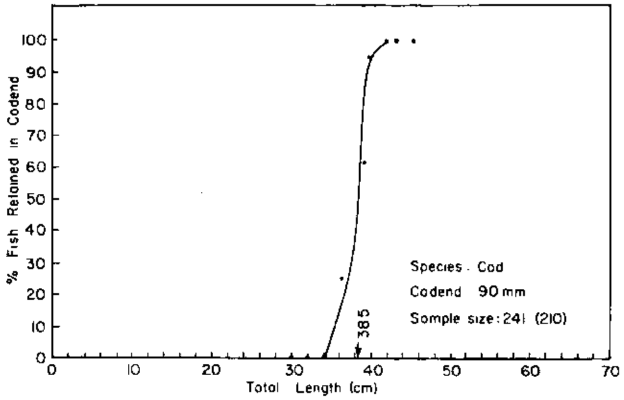

Fig. 5. Selection curve for cod from the joint mesh selection studies on the Scotian Shelf in 1977. (Other descriptors are the same as for Fig. 3.)

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[1] Fish lengths were expressed as fork length.

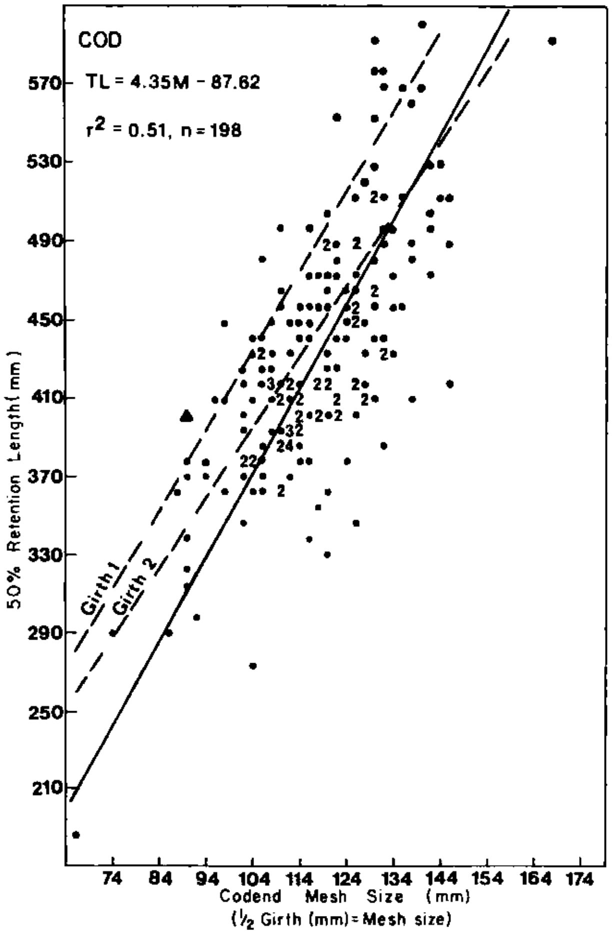

Fig. 6. General selection pattern for cod based on historical mesh selection studies. (Girths 1 and 2 are described in the text; other descriptors are the same as for Fig. 4.)

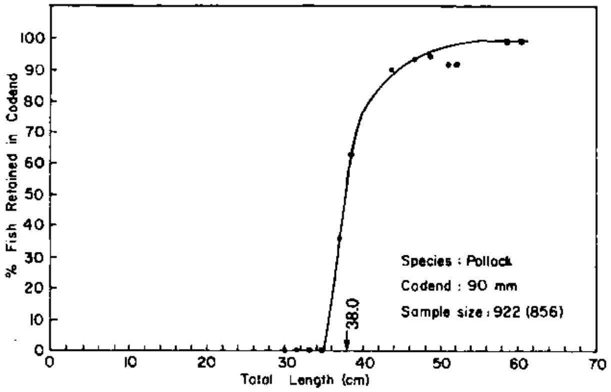

Fig. 7. Selection curve for pollock from the joint mesh selection studies on the Scotian Shelf in 1977. (Other descriptors are the same as for Fig. 3.)

Urophysis chuss, were estimated at 242, 190 and 465 mm for codend mesh sizes of 60, 70 and 120 mm respectively (Fig. 8). These points fall completely within the bounds of the historical haddock data (Fig. 4), a gadoid with similar soft body characteristics.

Selection curves for silver hake are discussed in detail by Clay (MS 1978). The general selection pattern based on historical data is defined by the regression

$$TL = 4.04\ M - 26.12 \qquad (r^2 = 0.77,\ n = 58)$$

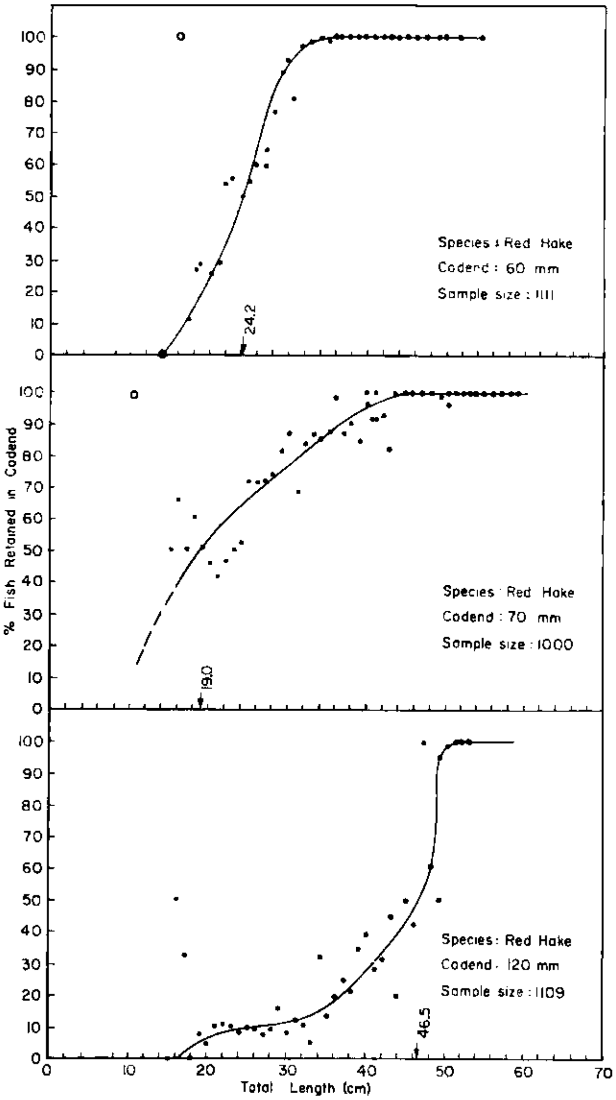

Fig. 8. Selection curves for red hake from the joint mesh selection studies on the Scotian Shelf in 1977. (Other descriptors are the same as for Fig. 3.)

which is illustrated in Fig. 9, together with the length-girth relationship, G = 0.48 TL - 1.99. The 50% retention lengths (triangles) show a trend in bias opposite to that observed for the gadoids noted above. This may be due to the softer, thinner body of silver hake when compared with that of cod and pollock.

Although not found on the Scotian Shelf, the whiting, *Merlangius merlangus*, is a gadoid for which much historical selectivity data are available from the Northeast Atlantic (Holden, 1971). The general selection pattern, defined by the regression

$$TL = 4.55\ M - 52.05 \qquad (r^2 = 0.69,\ n = 241)$$

and a length-girth relationship (G = 0.60 TL - 3.60), based on data reported by Gulland (1956) and Margetts (1954), are illustrated (Fig. 10) to further test the developing patterns of mesh selection. The regression line for the general selection pattern and the length-girth relationship (dashed line) follow the established pattern for other gadoids; the 50% retention length falls slightly below the length at which the girth equals twice the codend mesh size (stretched), at least over the range of codend mesh size to which most of the data apply.

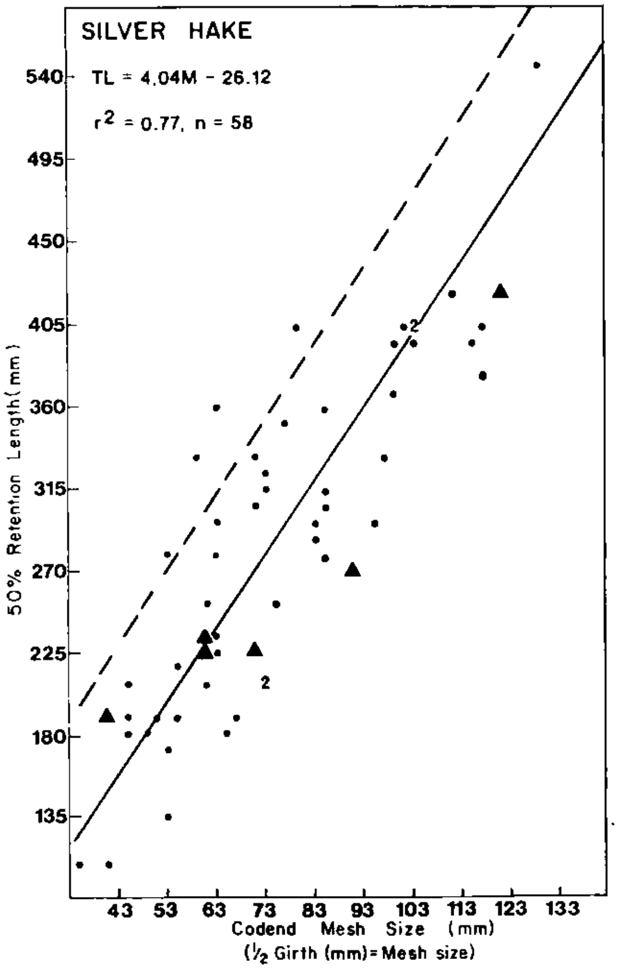

Fig. 9. General selection pattern for silver hake based on historical mesh selection studies. (Other descriptors are the same as for Fig. 4.)

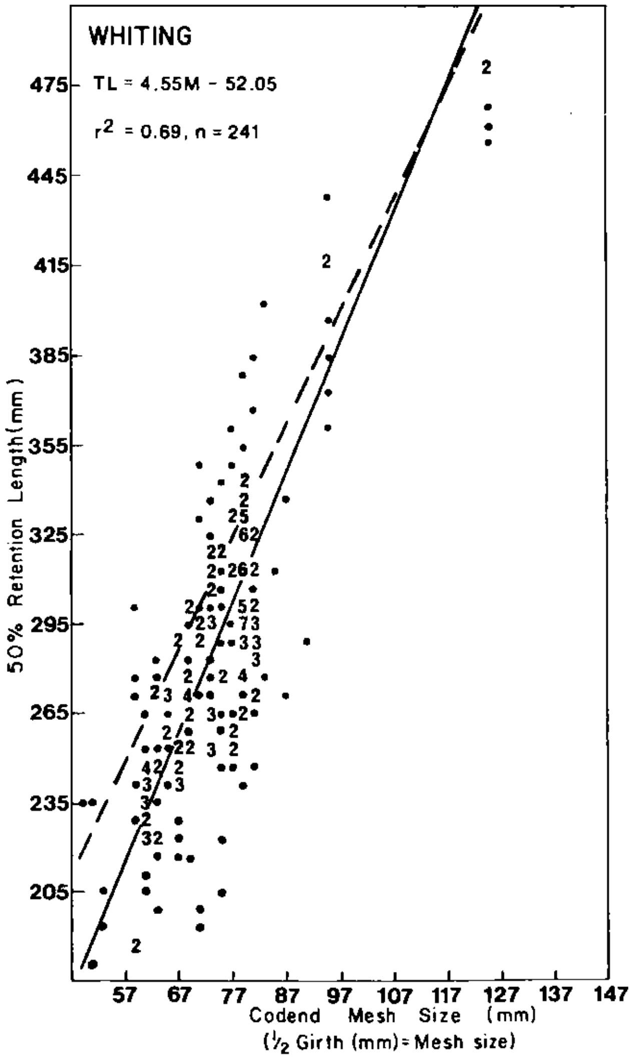

Fig. 10. General selection pattern for whiting based on historical mesh selection studies. (This species is not found in the Northwest Atlantic; other descriptors are the same as for Fig. 4.)

Atlantic redfish, *Sebastes* spp.

Selection curves for redfish from the 1977 co-operative studies (Fig. 11) indicate 50% retention

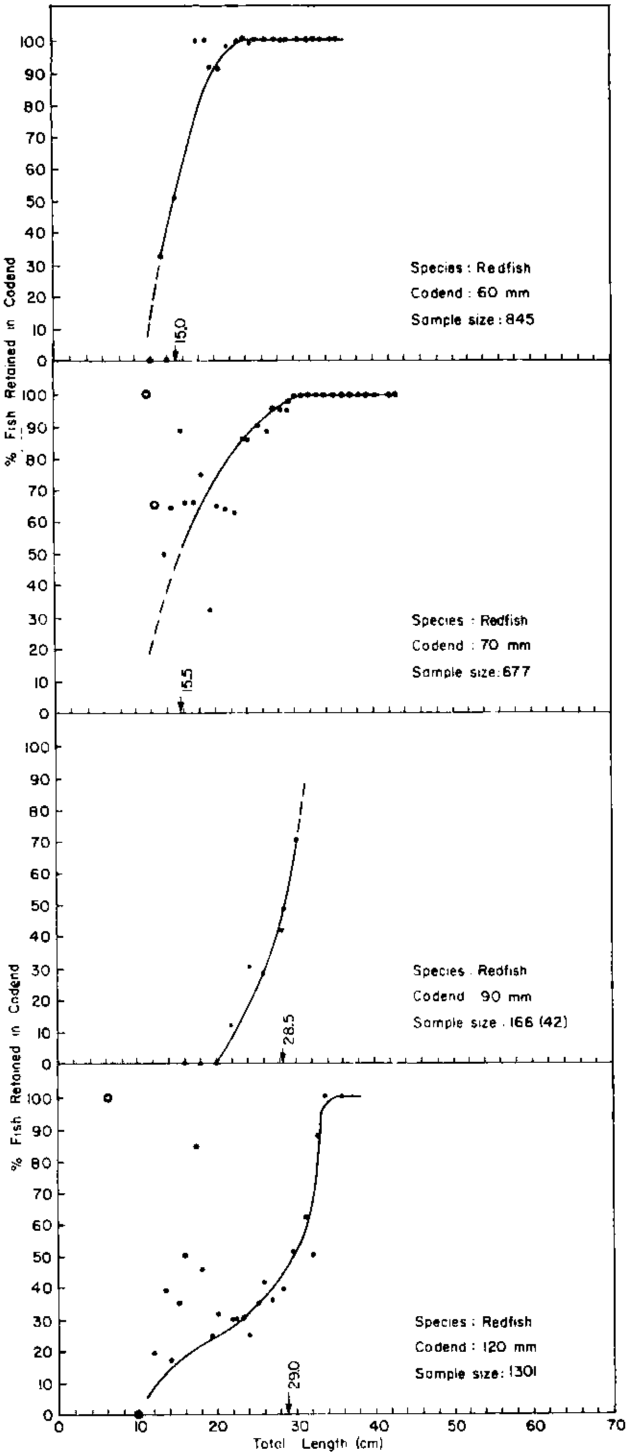

Fig. 11. Selection curves for redfish from the joint mesh selection studies on the Scotian Shelf in 1977. (Other descriptors are the same as for Fig. 3.)

lengths of 150, 155, 285 and 290 mm for codend mesh sizes of 60, 70, 90 and 120 mm respectively. The general selection pattern (Fig. 12) based on historical data is defined by the regression

$$TL = 3.50\ M - 94.96 \qquad (r^2 = 0.83,\ n = 78)$$

which is quite different in absolute values from those described above for gadoids. The length-girth relationship, from data collected by the author on the Scotian Shelf in 1978 (Fig. 13) and defined by the regression $G = 0.79\ TL + 0.16$ ($r^2 = 0.90$, $n = 50$), is very similar to that reported by Templeman (1963) in Newfoundland. Of the four points representing the

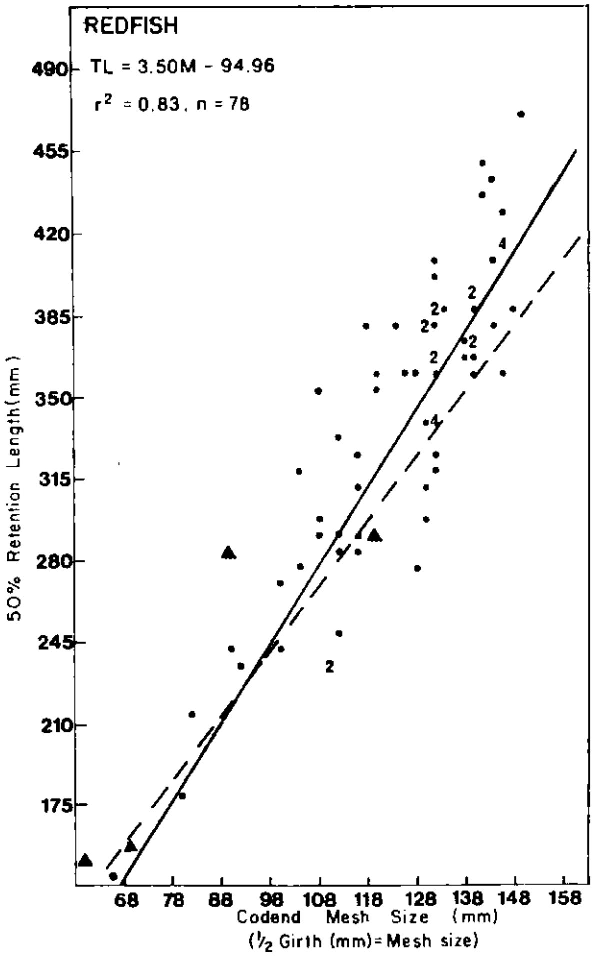

Fig. 12. General selection pattern for redfish based on historical mesh selection studies. (Other descriptors are the same as for Fig. 4.)

results of the 1977 studies (triangles in Fig. 12), that for the 90 mm mesh deviates from the general trend. This anomaly may in part be due to inadequate data. In contrast to the patterns for gadoid species, the length-girth relationship lies largely to the right and below the regression line defining the general selection pattern (Fig. 12). This indicates that the net is retaining larger fish than would theoretically be predicted from the length-girth relationship. The reason for this may be the firmer nature of the body of redfish and its numerous spines and bony protrusions of the opercula, constrast the smoother, softer bodies of gadoids.

Flatfishes

Little data were collected on selection of flatfishes during the two studies in 1977. For American plaice, *Hippoglossoides platessoides*, 50% retention lengths of 145, 162 and 300 mm were estimated for codend mesh sizes of 60, 70 and 120 mm respectively (Fig. 14), and the 50% retention lengths for witch flounder, *Glyptocephalus cynoglossus*, were 220 and 205 mm for 60 and 120 mm mesh codends (Fig. 15).

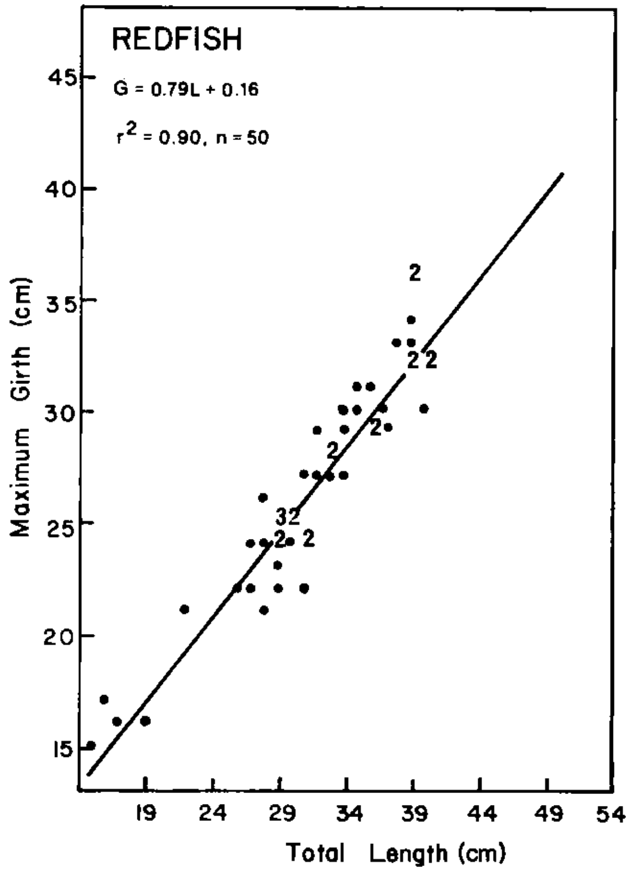

Fig. 13. Length-girth relationship for redfish from data collected by the author in a Canadian research cruise on the Scotian Shelf in 1978.

The general selection pattern for American plaice based on historical data is illustrated in Fig. 16, the regression line being defined by

$$TL = 2.32\ M - 3.29 \qquad (r^2 = 0.95,\ n = 25).$$

The general selection pattern for the European dab, *Limanda limanda*, is defined by TL = 2.38 M + 8.97 (r^2 = 0.46, n = 36). These data, together with historical data

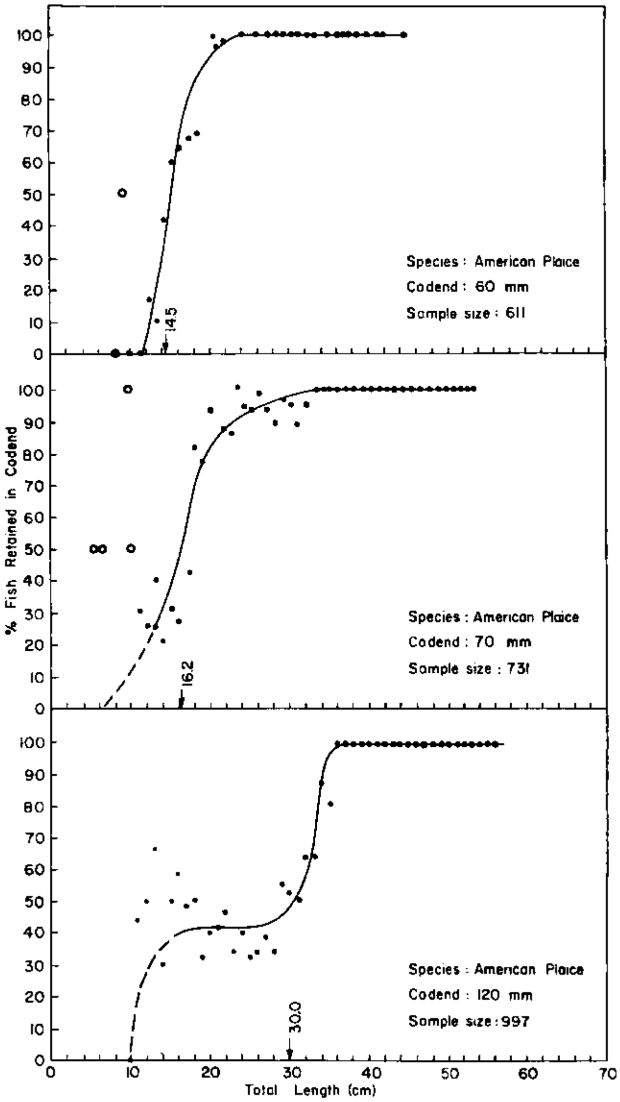

Fig. 14. Selection curves for American plaice from the joint mesh selection studies on the Scotian Shelf in 1977. (Other descriptors are the same as for Fig. 3.)

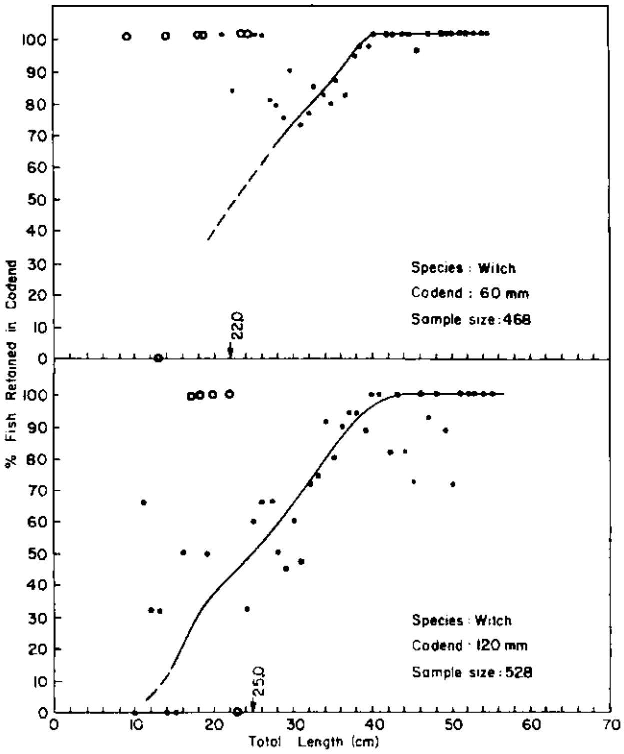

Fig. 15. Selection curves for witch flounder from the joint mesh selection studies on the Scotian Shelf in 1977. (Other descriptors are the same as for Fig. 3.)

for the yellowtail flounder, *Limanda ferruginea*, and current flatfish selection ogives, are shown in Fig. 17. The general selection pattern for these flatfishes is defined by the relationship

$$TL = 2.10\ M + 22.91 \qquad (r^2 = 0.92,\ n = 67).$$

The results of the 1977 studies for American plaice and witch flounder are indicated by the letters "A" and "W" respectively. In addition, the observations on witch flounder by Templeman (1963) are indicated by the letters "WT".

Pelagic species

From the limited amount of data collected for alewife, *Alosa pseudoharengus*, the 50% retention lengths were 180 and 240 mm in 60 and 70 mm mesh codends, and for mackerel, *Scombrus scombrus*, the 50% retention length was 160 mm in a 60 mm mesh codend (Fig. 18).

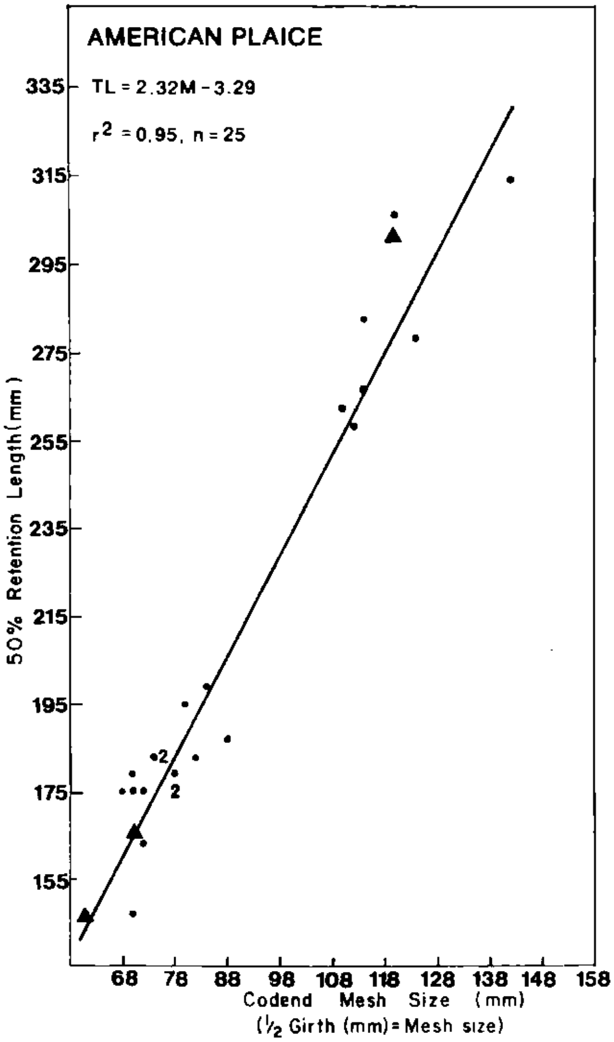

Fig. 16. General selection pattern for American plaice based on historical mesh selection studies. (Other descriptors are the same as for Fig. 4.)

Discussion

Graham (1954) proposed that mesh selection could be predicted from girth measurements, and since then various attempts have been made to utilize this concept for selection in otter trawls (Margetts, 1954; Gulland, 1956) and gillnets (Kondo, 1966; Berst, 1961; Kawamura, 1972). From the present review, it appears that the line representing the length-girth relationship runs approximately parallel to and above the regression line representing the general selection pattern, the extent of the separation of the lines being dependent on the firmness of the body. Exceptions to

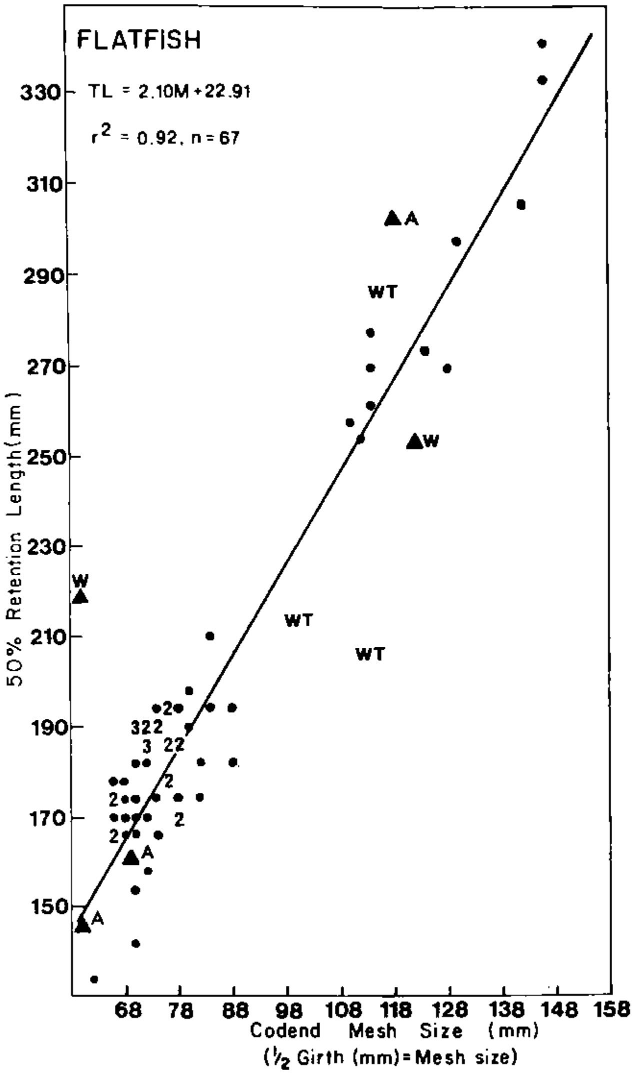

Fig. 17. General selection pattern for flatfish species based on historical mesh selection studies. (The 1977 results for American plaice and witch flounder are indicated by A and W, and Templeman's (1963) values for witch are indicated by WT; other descriptors are the same as for Fig. 4.)

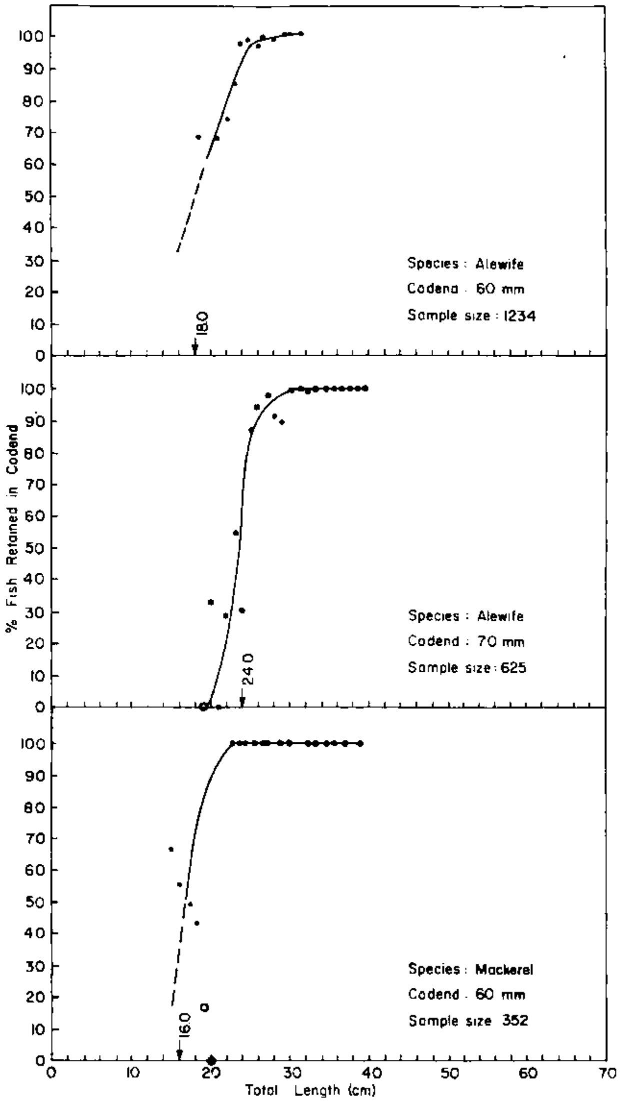

Fig. 18. Selection curves for alewife and mackerel from joint mesh selection studies on the Scotian Shelf in 1977. (Other descriptors are the same as for Fig. 3.)

this pattern are those species with bony protrusions which may inhibit escapement (e.g. redfish), and result in length-girth relationships which usually lie below the general selection pattern. In the absence of adequate mesh selection data, length-girth relationships may be used to approximate the general selection pattern over a range of mesh sizes and allow the estimation of selection factors for the species concerned.

For comparison of the general selection patterns of the various species considered in this paper, the regression lines are plotted in Fig. 19. It appears that the gadoid species investigated can be considered as having similar selection patterns. Although the lines for cod and haddock have different slopes, they are quite close over the range of codend mesh sizes applicable to management of the Scotian Shelf fisheries. The regression line for redfish deviates significantly from those of the gadoid species, the reason for this being the shape of the body and the bony structures of the head. The lines for the flatfishes are very different in slope from those of the gadoids and redfish.

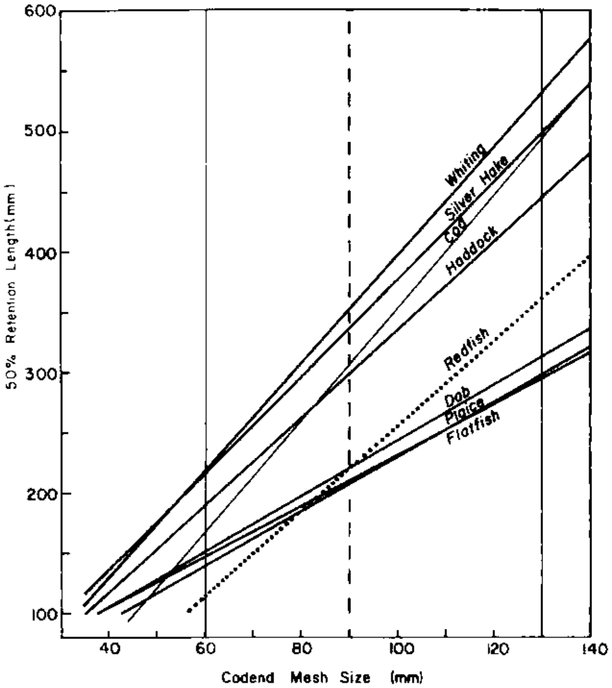

Fig. 19. General selection patterns (regression lines) for all fish species considered in this paper. (The vertical lines represent the current minimum 60 mm mesh for silver hake, the minimum 130 mm mesh for other groundfish species, and the proposed minimum 90 mm mesh (Clay, 1979) to replace the 60 mm mesh size in use for silver hake on the Scotian Shelf.)

Most of the 50% retention lengths for the various fish species sampled on the Scotian Shelf in 1977 fit the historical selection patterns reasonably well. Exceptions, such as the 50% retention length for witch flounder in the 60 mm mesh codend (Fig. 17), are probably due to small numbers of fish in the selection range. The most valuable result of this analysis is the possibility of utilizing past studies on species of interest to produce "general selection patterns" which may be useful in analyzing the effects of mesh regulations on species of fish having similar body form but for which no mesh selection data are available. Such a selection pattern for a species could be considered as a valid "commercial average". The inherent variability in mesh selection studies raises the question of the necessity and value for further studies on species for which much data already exist. In the case of species for which selection studies are not well documented, the possibility exists of estimating a "commercial average" general selection pattern from the length-girth relationship, if some assumptions are made about the shape, smoothness and firmness of the body.

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Density-Dependent Processes and Management Strategy for the Northwest Atlantic Harp Seal Population[1]

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Abstract

Density-dependent factors are essential to the stability of the size of natural populations. Three such factors, namely, age of whelping, pregnancy rate and pup mortality rate, are modelled and investigated for the Northwest Atlantic harp seal population. Variable pup mortality has a pronounced effect upon the shape of the sustainable yield curve. The maximum sustainable yield is estimated at 215,000 animals, of which 80% are pups, and the corresponding population size is 1.4 million. These results are compared with previous estimates by other investigators and with estimates obtained by varying the assumptions about density-dependence in the modelled population. The estimates of maximum sustainable yield and the corresponding population size are generally lower than estimates derived from models with fewer density-dependent controls.

Introduction

To study density-dependent mechanisms in wild mammal populations, it is necessary to select species which have fluctuated widely in abundance during periods of intense biological sampling. The Northwest Atlantic harp seal, *Pagophilus groenlandicus*, is one such species (Sergeant, MS 1976a; Lett and Benjaminsen, 1977). Although catch statistics are available for this population as early as the 18th century (Chafe *et al.*, 1923), biological sampling did not begin until the early 1950's (Fisher, 1952; Sergeant, 1959; Sergeant and Fisher, 1960). This was a particularly opportune time to begin sampling, as the population had increased during and after World War II to a high level, estimated at 2.3 million seals (Lett and Benjaminsen, 1977). The sampling initiated at that time has continued and was intensified after 1960. In addition to catch-at-age information from the various fisheries, much data have been collected on maturity and fertility (Fisher, 1952; Sergeant, 1966, MS 1969, MS 1976a; Øritsland, MS 1971), on migration patterns (Sergeant, MS 1976a), on feeding habits (Sergeant, 1973a; Kapel, MS 1975), on population census (Sergeant, MS 1975; Lavigne *et al.*, MS 1977), and on mortality and sex ratios (Ricker, MS 1971; Ulltang, MS 1971; Benjaminsen and Øritsland, MS 1975; Lett and Benjaminsen, 1977).

Historically, harvesting levels on this stock have been particularly high. For example, the offshore harvest alone exceeded 450,000 seals during the period from 1830 to 1850, reaching a peak level of 687,000 animals in 1844. The average harvest was much lower (about 150,000) during the early 1900's. Recovery of the stock occurred during the wars of 1914–18 and 1939–45. Hunting again became intense after World War II, especially after Norwegian vessels joined the hunt and took large numbers of adult females, which caused a rapid decline in the stock (Lett and Benjaminsen, 1977). Quotas were initiated in 1972 and the stock has been increasing since then (Benjaminsen and Øritsland, MS 1975; Lett and Benjaminsen, 1977). However, the more important observation is that this stock has maintained an average annual yield of 275,000 animals over the past 150 years.

How has this population been able to survive for so long under such intense harvesting? The response to that question is the theme of this paper. Density-dependent mechanisms, possibly operating at behavioural and physiological levels, have given the stock resilience and stability in the face of widely varying annual exploitation. Indeed, it is upon the knowledge of these density-dependent mechanisms that much of our management advice hinges.

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Biological Sampling of the Stock

The stock

The harp seal, as a species, reproduces in three widely separated populations located on pack ice around Newfoundland, Jan Mayen Island, and in the White Sea. Studies of skull and body dimensions (Khuzin, 1963, 1967) have shown that the Newfoundland, or western Atlantic, population is more distinct from the two eastern Atlantic populations than the two eastern populations are from each other. Sergeant (1976b) indicates that there is limited intermixing between the eastern and western populations.

The Newfoundland population is divided into two sub-populations, one reproducing on the southward

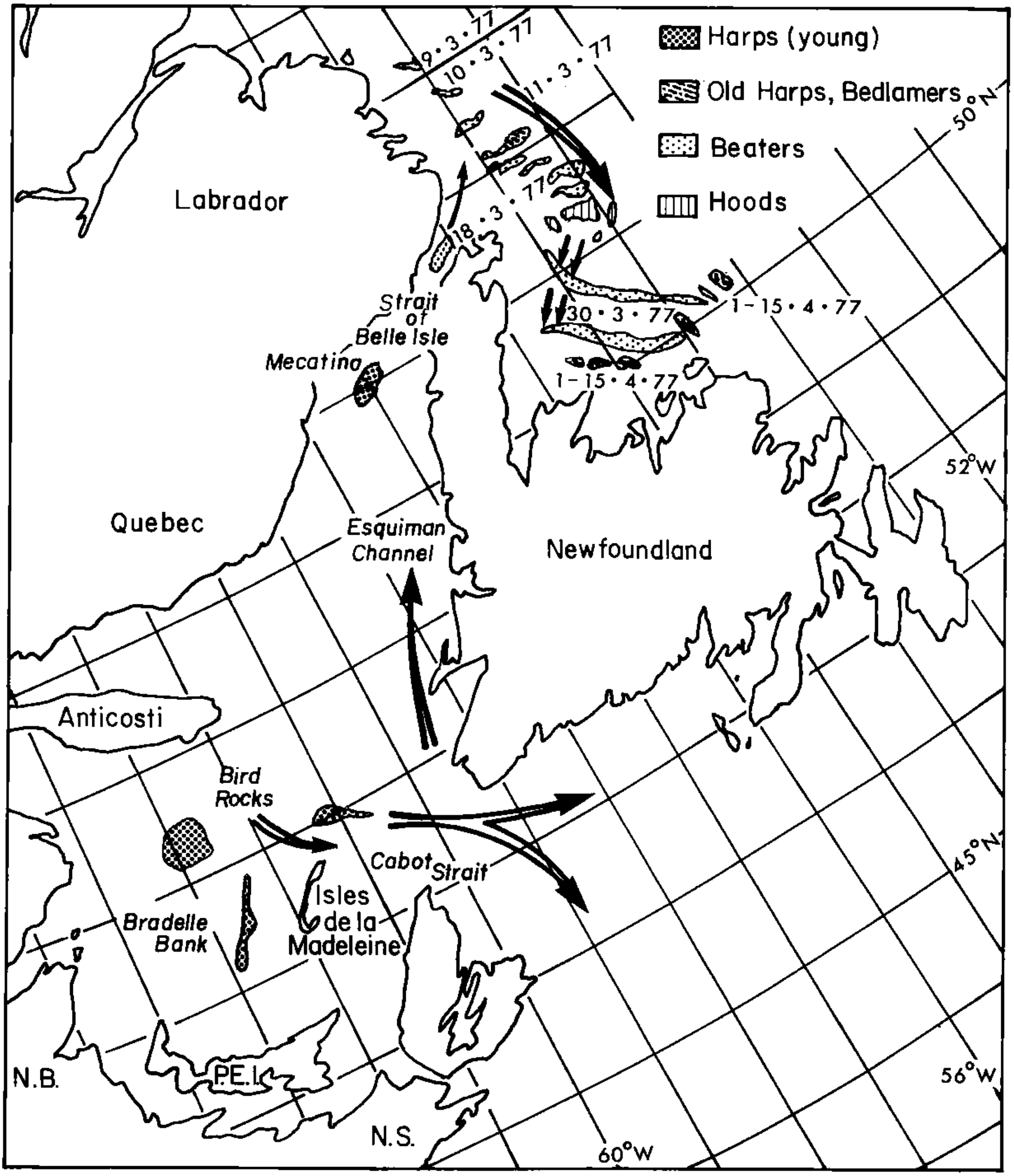

Fig. 1. Map showing movements of harp and hooded seals in the Northwest Atlantic.

drifting pack ice off southern Labrador and the other in the Gulf of St. Lawrence (Fig. 1). The herd which reproduces off Labrador in the spring (known as the Front herd) can further be divided into a northern and a southern contingent. The position of the whelping patches depends on the food supply and the formation of rather loosely-packed ice interspersed with sufficient leads of water. In early March (about 8th or 9th), the younger females, which have less control over parturition than older animals, get on the ice to give birth. The older females remain in the area of abundant food for approximately two more days after which they too begin to whelp. This gives the impression of two sub-herds, since the younger animals have drifted about 50 km farther south by the time that the older animals begin to whelp (Lett and Benjaminsen, 1977).

In the Gulf of St. Lawrence, whelping begins as early as 22 February and continues until 21 March (Lett *et al.*, MS 1977). The herd may become divided into as many as three sub-herds. Whelping usually begins on the edge of the ice east of Anticosti Island. This sub-herd then drifts southward to the Bird Rocks just northeast of the Magdalen Islands. The period of whelping is protracted, however, and the sub-herd never seems to produce many more than 10,000 pups, because whelping animals drift out of the Gulf on the moving ice. Another sub-herd begins to form about 3 March in the Bradelle Bank area to the west of the Magdalen Islands. This is the largest concentration of seals and is usually that which is exploited (Lett *et al.*, MS 1977). The only other sub-herd on record is that called the Mecatina Patch which forms along the south shore of Labrador in the northern part of the Gulf (Fig. 1). The whelping dates for this sub-herd are similar to those of the Front population, and these seals may therefore be part of the Front breeding colony. In former years, this patch has been reported to have contained from 20,000 to 40,000 animals, but no proper census has ever been made because there has been no assurance that the herd would form from one year to the next. Factors relating to the whelping of harp seals in this area are still unresolved.

Following the whelping period at the Front, the seals move southward into Notre Dame Bay on the northeast coast of Newfoundland (Fig. 1). The pups lose their fetal hair and take on the spotted juvenile appearance of "beaters". It is in this area that one of the major hunts takes place by Newfoundland landsmen in small motor boats and larger vessels up to 20 m in length. In addition to beaters, large numbers of immature bedlamers and adults are taken, especially when these animals begin to concentrate on feeding shoals before their movement to the molting areas. Once the molt begins, the seals swim northward until they reach the pack ice, usually east of the Strait of Belle Isle. After molting, which takes 3–4 weeks, the adults migrate northward to the Canadian Arctic and northwestern Greenland.

The pattern of movement in the Gulf is somewhat different. The beaters and adults usually move eastward to Cabot Strait and then begin their northward migration along the west coast of Newfoundland, where there is also a substantial kill of beaters and juveniles. Molting sometimes takes place in the vicinity of Esquiman Channel (Fig. 1) but this is highly variable. The molting patch may be seen in an area on one day and be gone on the next, the next sighting of the herd being many kilometers away from the last one. Within 3 to 4 weeks after the beginning of the molt, the seals disappear completely from the Gulf of St. Lawrence.

The beaters and juveniles, following the northerly progression of the annual spring zooplankton bloom, find their way to Baffin Bay (Sergeant, MS 1976b). At this time, the mature and immature harp seals are fairly well segregated, with the matures mainly in the Canadian Arctic. It is not known exactly why this segregation occurs, but Sergeant (1973a) postulates that the younger seals feed on capelin, *Mallotus villosus*, and shrimp, *Pandalus borealis*, off West Greenland while the adult seals concentrate on larger food items.

The distinctness of the Gulf and Front populations as separate breeding stocks and the degree of gene flow is interesting biologically and important to the development of a realistic harvesting strategy. Sergeant (MS 1977) presented detailed information indicating that there is substantial intermixing between juveniles of the Gulf and Front herds (79% for age 1, 69% for age 2, 11% for age 3) but that there is no intermixing of adults. It is known that seals which would normally have whelped in the Gulf have done so at the Front when there was no ice in the Gulf (Lett *et al.*, MS 1977). Thus the distinctness of the two breeding herds is still unresolved.

Age composition data

Catch-at-age data form the basis of the assessment of most animal populations. Such data for the harp seal fishery in the Northwest Atlantic during 1974–77 are given in Table 1. Data for 1952–74 are listed in Lett and Benjaminsen (1977). The determination of the real catch-at-age structure is a formidable problem in itself for this fishery because of its diversity. The problem consists of producing a weighted catch-at-age frequency of the total annual catch of age 1 and older seals by amalgamating the age frequencies from the various fisheries in their proper proportions.

TABLE 1. Age composition of the catches of harp seals in the Northwest Atlantic, 1974–77. (Catch-at-age data for 1952–74 are given in Lett and Benjaminsen (1977).)

Age	Age composition of catch (numbers)			
	1974	1975	1976	1977
0	118,036	140,629	132,085	124,932
1	9,604	9,629	10,928	5,448
2	5,629	5,719	6,241	4,898
3	2,123	3,275	3,976	4,271
4	1,752	1,999	2,874	3,154
5	1,945	2,072	1,567	1,677
6	3,144	1,867	1,264	1,163
7	985	1,632	1,073	921
8	1,200	1,186	1,027	743
9	1,283	740	481	357
10	954	693	757	236
11	732	672	523	259
12	891	605	369	161
13	825	646	306	266
14	685	529	309	368
15	674	353	517	335
16	686	350	191	64
17	594	247	221	35
18	447	323	145	131
19	377	159	135	29
20	306	127	155	128
21	282	88	40	50
22	287	106	46	35
23	201	59	53	29
24	219	97	31	27
25	210	74	30	22
Total (1+)	36,035	33,447	33,259	24,817

Samples of seals shot in Notre Dame Bay, Newfoundland, consist primarily of animals which have not fully developed their adult characteristics, namely bedlamers. The net fisheries at La Tabatière, Quebec, and southern Labrador yield samples of pregnant females and mature males as they migrate southward into the whelping areas. However, the samples from these areas in January show a preponderance of seals which will whelp for the first or second time, these animals arriving later than the older ones. Samples taken at St. Anthony, Newfoundland, seem to better represent the population age structure, but separate catch statistics are not always available for these areas on the same scale as the sampling data. However, when such data were available, they indicate that, on the average, each of these fisheries tends to be roughly equivalent in terms of the overall catch. Therefore, the catch-at-age frequencies were summed without weighting to produce a catch-at-age composition for the yield by landsmen without serious error (Table 1, Lett and Benjaminsen, 1977).

The catches by large vessels from the breeding areas and molting patches have a considerably different age structure from that by landsmen and they must therefore be treated separately (table 1, Lett and Benjaminsen, 1977). There is usually a high representation of age 1 and age 2 seals in these samples, basically because there animals are segregated around the periphery of the adult herd and are more accessible to hunting. The overall age composition of the landsmen catch must be combined with that for age 1 and older animals exploited by the larger vessels, weighting each frequency in accordance with their respective catches. If this procedure is not followed, a serious consistent bias would result, especially in the data for the last 15 years, due to the increased interest of Newfoundland in the fishery (fig. 2, Lett and Benjaminsen, 1977).

Between 1952 and 1960, jaws of seals for age determination were collected on a regular basis from the landsmen's catch and this sector of the hunt may be considered as being well sampled (Sergeant and Fisher, 1960). During 1952–54 and 1957–59, samples of jaws were collected from the catches of large vessels. However, these samples were inadequate in 1957 and 1958, and it is unlikely that they accurately represent the catch. For this reason average catch-at-age frequencies were used to represent the catch composition of the large vessels. The attendent errors are possibly serious, since the catch of age 1 and older animals by large vessels represented between 87 and 96% of the total catch during this period. Sampling steadily improved after 1961, the catches from the molting patches by large vessels and the catches by landsmen being well represented in the samples. Annual catch-at-age data for 1961 and onwards were obtained from various sources (Sergeant, personal communication; Øritsland, MS 1971; Benjaminsen and Øritsland, MS 1975). Sampling of both the landsmen and the large vessel catches was inadequate in 1972, but the available data are included in this analysis.

Samples of the West Greenland and Canadian Arctic catches, which represent an average of about 8% of the total catch, are excluded from this analysis, since no consistent sampling and catch records are available.

Shot samples of males from the molting patches are used to estimate natural mortality. However, as noted above, age 1 seals are usually segregated from the remaining age-groups and are not consistently sampled in the molting patches (Benjaminsen and Øritsland, MS 1975). Furthermore, the closing date of the hunt affects this sample; the earlier the hunt in the molting patch is terminated, the lower is the proportion of females in the catch (Sergeant, 1965; Øritsland, MS 1971). Thus the age composition of adult seals varies, depending on the duration of the hunt, with the samples consisting mainly of male animals. At age 2 the sex ratio is about 50:50, but by age 10 about 80% of the molting animals sampled are male (Fig. 2). This is primarily because many of the adult females remain in the water and are feeding to regain the energy lost during whelping and suckling.

Determination of Biological Relationships and Estimation of Parameters

The instantaneous rate of natural mortality (M)

The most elusive vital rate in population dynamics is usually natural mortality. Since the exploitation rate of age 1+ seals is very low, currently about 0.015 (Lett *et al.*, MS 1977), the annual decline in numbers of these age-groups is primarily due to natural mortality.

Natural mortality was estimated using pup production determined by the survivorship method (Benjaminsen and Øritsland, MS 1975, MS 1976; Sergeant, MS 1975), information on maturity, sex ratio, pregnancy rate, and the age composition of seals in the molting patches. The analysis assumes that there is no difference between the natural mortality rates of male and female harp seals. The validity of this assumption is based on the observation that males and females have similar growth rates and achieve equivalent maximum ages (Sergeant, 1973a). Since Lavigne *et al.* (MS 1976) indicate that the metabolic rate and body size of seals are well correlated and Simms *et al.* (1959) indicate that mortality and metabolic rates of animals are related, it is unlikely that male and female seals have different natural mortality rates.

The age structure of the population was determined from samples of the catches by large vessels in the molting patches, as given in Lett and Benjaminsen (1977) and Sergeant (MS 1977). These catch-at-age frequencies were multiplied by the proportion of males at different ages (Fig. 2) to give an estimate of the population structure of age 2+ animals. However, since partial recruitment may vary somewhat from year to year, only the data for age-groups 5-22 were used to calculate natural mortality.

With a knowledge of the maturity, sex ratio, pregnancy rate and population structure, the pup production could be estimated for the appropriate age-groups. It was assumed, as in Lett and Benjaminsen (1977), that 6% of the breeding females are older than age 25. The natural mortality (M) for each age-group was therefore calculated by the formula

$$M = ln\left(\frac{{}_{a}N_{t} - {}_{a}C_{t}}{{}_{a+1}N_{t+1}}\right) \qquad (1)$$

where ${}_{a}N_{t}$ is the number-at-age in year t, and ${}_{a}C_{t}$ is the catch-at-age in year t. For the period 1966-77, M for age-groups 5 to 22 was estimated to be 0.10 with a standard error of 0.03. The maturity was estimated by linearly interpolating the reported ogives for 1966 and 1977.

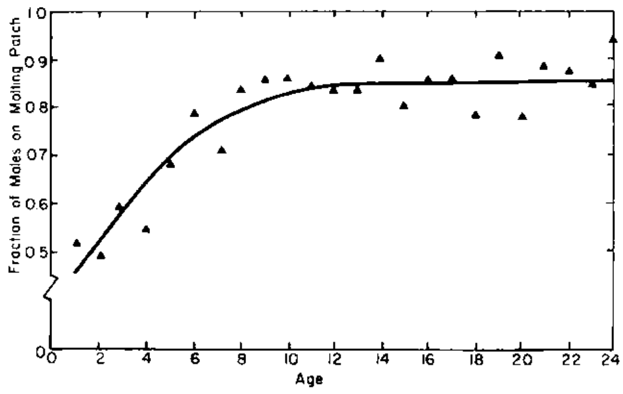

Fig. 2. Proportion of males by age-group in Norwegian catches of molting harp seals in the Northwest Atlantic, 1969-74. (From Benjaminsen and Øritsland, MS 1975.)

Using the method devised by Ricker (MS 1971), Benjaminsen and Øritsland (MS 1975) calculated natural mortality to be 0.102 with a standard error of 0.011. Further consideration of these data resulted in a revised estimate of M = 0.106 (ICNAF, 1978). Lett and Benjaminsen (1977) estimated natural mortality to be 0.114 by a rather suspect method, and Winters (MS 1976) calculated M to be 0.115. Earlier estimates were somewhat lower; both Ricker (MS 1971) and Ulltang (MS 1971) estimated natural mortality at about 8% per year, while sergeant and Fisher (1960) estimated the total mortality to be as low as 0.079 for the 1952-54 period. The available evidence indicates therefore that the natural mortality for harp seals is about 0.10 and this value was used in the analysis.

No evidence for age-dependent natural mortality could be found in the present analysis. This is not surprising considering the uncertainties in the data and the delicate changes possibly exhibited by this parameter (Lavigne *et al.*, MS 1976). Since more detailed data of this kind exist for the harp seal population than perhaps for any other stock of large mammals, the assumption of constant mortality for age 2+ seals is considered justifiable on the basis of the analysis. An important management consideration, however, would be the mortality in the first year and whether it varies in relation to some density-dependent mechanism, as suggested by Lett and Benhaminsen (1977).

Sequential population analysis

Sequential population analysis is a method of estimating the number in a population by age for a period of years from catch-at-age data (Fry, 1949; Murphy, 1964; Jones, 1964; Pope, 1972). The analysis of a year-class starts with an estimate of the number alive in the last year for which catch data are available for that year-class (terminal year-class size) and proceeds to estimate the numbers in previous years by adding estimated annual losses due to hunting and natural mortality. Inputs into the model are therefore the catch-at-age data, an estimate of the natural mortality coefficient and estimates of the terminal year-class sizes. For the harp seal population, catch-at-age data (ages 1-25) for the years 1952-77 and M = 0.10 were used. Estimates of the sizes of the 1952-76 year-classes in 1977 and of the 1927 to 1951 year-classes at age 25 were needed. The calculated numbers-at-age relate to the time of whelping. Since most of the hunt takes place shortly after whelping, it is assumed that hunting mortality is instantaneous and independent of natural mortality. Therefore, the numbers-at-age were calculated by the equation

$$ {}_{a+1}N_{t+1} = ({}_{a}N_{t} - {}_{a}C_{t}) \exp(-M) \tag{2} $$

which corresponds to the assumptions in Pope's (1972) cohort analysis. Since the analysis works backward from the oldest age, the equation is used in the following form:

$$ {}_{a}N_{t} = {}_{a}C_{t} + {}_{a+1}N_{t+1} \,.\, \exp(+M) \tag{3} $$

For each succeeding estimate, the size of the year-class is increased to account for natural mortality and the catch is then added.

Terminal year-class sizes can be estimated either directly or by using an estimate of the exploitation rate to calculate the year-class size from the catch data. For the 1951-76 year-classes, it is possible to estimate the year-class sizes in 1977. For the 1926-50 year-classes, exploitation rates at age 25 were estimated. The age structure of the population in 1977 can be estimated by applying sex ratio data for seals in the molting patch to the catch-at-age sample taken in the molting patch by large vessels in 1977. If sex ratios in the population, pregnancy rate and whelping ogive are known, this population structure can be used to calculate the population size to give any particular number of pups. With an estimate of the latter, numbers-at-age in 1977 can be estimated and hence the terminal sizes for the 1951-76 year-classes.

An iterative method was used to estimate terminal exploitation rates for the other year-classes. It was assumed that the selectivity of 25-year-olds in the hunt had not changed relative to the selectivity of all seals over the age of 10. Thus the ratio of the exploitation rate on 25-year-olds to the average exploitation rate on age 1+ seals was kept approximately constant from 1952 to 1977. Once the numbers-at-age are estimated, the pup production can be estimated for each year, as was done for 1977. With independent estimates of pup production, the exploitation rate can be adjusted until the two estimates agree. Such estimates were derived by Winters (personal communication) from survival indices. The Y on X regression values were used since the X variable (pup catch) probably has a much smaller variance than the Y variable (survival indices). These values with 90% confidence limits on two of the points are given in Table 2.

TABLE 2. Estimates of pup production in the Northwest Atlantic from sequential population analysis and those derived by Winters (unpublished data) from survivorship indices.

	Estimates of pup production from	
Year	Sequential pop. analysis	Survivorship indices
1952	566,323	666,000[a]
1953	550,422	530,000
1954	555,380	549,000
1955	554,578	572,000
1956	557,712	531,000
1957	556,217	528,000
1958	547,560	517,000
1959	512,450	495,000
1960	493,828	492,000
1961	464,710	483,000
1962	430,747	466,000
1963	401,433	423,000
1964	379,204	380,000
1965	360,720	397,000
1966	363,435	396,000
1967	357,433	393,000
1968	362,502	406,000
1969	368,569	390,000[b]
1970	361,750	381,000
1971	348,087	379,000
1972	330,996	–
1973	330,520	–
1974	318,239	–
1975	308,931	–
1976	313,517	–
1977	330,000	

[a] 90% confidence limits are 477,000-2,127,000.

[b] 90% confidence limits are 332,000-497,000.

For the calculation of pup production, the sex ratios in the population derived by Lett and Benjaminsen (1977) were used. Pup production in 1977 was assumed to be 330,000 animals, which is in the range of values agreed upon as being the most realistic by the Marine Mammals Subcommittee of the Canadian Atlantic Fisheries Scientific Advisory Committee. A pregnancy rate of 0.92, a mean age of whelping of 4.5 years and the whelping ogive derived by Lett *et al.* (MS 1977) were used to derive an initial set of numbers-at-age. The exploitation rates on 25-year-olds were then adjusted as noted in the foregoing paragraph. With this set of values, density-dependent functions for mean age of whelping and fertility rate were derived and the analysis was repeated until the reuslts stabilized. The pup production estimates of Winters (Table 2) were not reproducible using the assumed starting population structure in 1977 without extreme variation in exploitation rates. The population structure was therefore altered slightly to increase the proportions of older seals (10% increase for age 25, 9.6% for age 24, 9.2% for age 23, etc.). The proportions were then renormalized to add to 100%.

The estimated pup productions during 1952-77, given in the first column of Table 2 and illustrated in Fig. 3, do not show the amount of variation exhibited by Winter's data but follow the same trend. Final numbers-at-age from the sequential population analysis are given in Table 3 and the exploitation rates for age 25 seals and the averages for age 1+ and age 11+ animals are given in Table 4.

To develop the density-dependent functions, an estimate of the population of age 1+ animals was needed for 1947. There are catch data but no age

TABLE 3. Population structure (numbers-at-age) of the harp seal stock in the Northwest Atlantic, 1952-77, derived from sequential population analysis.

Age	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964
1	211989	207052	210697	184239	163758	201306	170463	169800	189984	234573	247556	146708	191684
2	255436	187582	168632	158657	143176	134905	159087	113640	130858	137658	206291	199035	126612
3	269909	220696	163826	139809	132250	123059	111394	125216	92169	101919	122208	155756	172145
4	183522	237357	194366	144384	119695	115850	105349	89184	107261	74252	89898	101827	133656
5	140226	160644	211229	170039	125697	105269	100048	85020	75998	88470	84331	72703	87631
6	305596	120661	141748	187879	149571	111328	91407	82236	72984	62904	79086	51778	61971
7	102839	265630	106277	124453	166481	133247	97434	75246	70938	60806	55710	68907	42713
8	145309	85406	237760	92653	109563	148731	117621	81998	65041	59774	53820	47714	58451
9	97301	123969	74754	212120	80967	97286	131946	100756	71462	55051	53352	45910	39238
10	125841	82713	109700	65608	189592	71630	85659	114552	88697	61280	49115	45594	37928
11	96067	107793	72794	96301	57180	170113	62557	72775	101402	77084	54370	43219	37109
12	66258	81596	95055	64646	85183	50492	151857	52303	63887	88907	69104	47873	35089
13	102265	58378	72326	83439	56656	75856	43796	133670	45551	55187	80076	60650	40357
14	61374	91147	51676	62904	73903	50207	66939	36198	119328	38839	49564	71406	51766
15	72773	53430	81572	45465	55417	65864	43792	57475	31178	105721	34779	43445	61388
16	135448	62040	46618	72106	39720	49271	58085	36783	50563	26163	95476	29371	36751
17	20453	121253	54416	39996	63901	35030	43188	50046	31944	43786	23379	85657	24549
18	18216	16376	108452	48250	35004	57035	30460	36756	44092	27174	39395	19499	75375
19	19157	14814	14022	97778	42608	30890	50517	25581	32238	38362	24470	34819	16267
20	19213	16463	12825	11563	87507	37889	26944	43976	22174	27778	34587	21552	30381
21	12876	12887	12376	10930	9685	78815	33411	22805	39019	18912	24960	29966	18319
22	5679	10399	10185	10876	9280	8357	70504	29191	20077	34470	17064	22419	26113
23	28075	5084	8587	8910	9305	8042	7005	62884	25917	17414	31095	14794	19503
24	14991	24968	4013	7070	7684	8129	6899	5576	56495	22894	15686	27956	12737
25	19396	12348	22168	3495	6083	6715	7020	5608	4735	50655	20656	14028	24783
1+	2530208	2380687	2286094	2143570	2019865	1975117	1873365	1709280	1653991	1610054	1636029	1502585	1462517
2+	2318219	2173635	2075398	1959330	1856107	1773811	1702922	1539460	1464007	1375481	1388473	1355878	1270633

Age	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
1	166069	113727	88140	82823	211945	101990	99206	139219	239673	213299	210180	211166	190463
2	171179	143558	92446	69910	69530	172788	85187	83147	125075	215102	184311	181466	181183
3	110566	151548	120502	79034	59167	60205	149527	74834	74068	110572	189539	161597	158550
4	150005	95612	132436	107262	68736	50742	52020	132953	65656	64747	98129	168538	142621
5	114215	129932	81815	117942	95405	59922	43521	46017	118878	57520	57001	86982	149899
6	74438	96207	112247	70602	105196	83642	52060	38248	40187	104519	50286	49702	77286
7	49104	60705	81545	97258	82335	93263	74156	46414	33667	35238	91728	43812	43828
8	34923	41607	50066	69857	85798	54160	82781	66551	41255	29288	30993	81341	38672
9	49795	29948	34442	42534	60949	74934	47525	74413	59537	36081	25415	26971	72671
10	32619	44079	25272	29149	36943	53045	65953	42300	66735	52745	31486	22327	23969
11	30020	28136	38139	21211	24766	31771	46226	58919	37513	59445	46863	27863	19517
12	31228	26571	23176	32445	18007	20920	27584	41325	52776	32684	53128	41795	24736
13	29448	26367	22453	19550	26425	15250	17724	24411	36656	46524	28767	47523	37484
14	34686	26048	22375	19126	16806	24548	12736	15594	21588	32241	41350	25445	42724
15	45041	29980	21918	18570	16190	14001	21448	11273	13788	18571	28553	36936	22744
16	53013	39475	25728	18195	15824	13389	11573	19104	9830	11511	16194	25517	32953
17	31160	47250	34288	22113	15525	13421	11288	10203	17011	8072	9795	14336	22916
18	19800	27732	41755	29248	19192	12918	11377	9957	8993	14775	6766	8839	12772
19	64321	16970	23628	36341	25346	16425	10983	9972	8806	7573	12965	5830	7686
20	12609	57330	14418	19924	31912	21991	14226	9711	8880	7492	6512	11567	5153
21	27362	11102	50864	12012	17357	28036	19286	12581	8559	7523	6503	5777	10344
22	14595	24221	9340	45423	10430	15090	25016	17267	11264	7475	6552	5804	5191
23	22605	12951	21601	6006	40482	8936	13372	22377	15539	9568	6504	5832	5210
24	16625	20401	11097	19046	6902	36185	7918	11892	20187	13679	8476	5831	5229
25	10063	14964	18123	9879	16992	6003	32565	7048	10711	18129	12360	7581	5248
1+	1395289	1318419	1197633	1097261	1160179	1063577	1035259	1025730	1147034	1214571	1260350	1310197	1339052
2+	1229220	1202692	1109493	1014436	948233	981587	936052	886511	907361	1001272	1050170	1099031	1148588

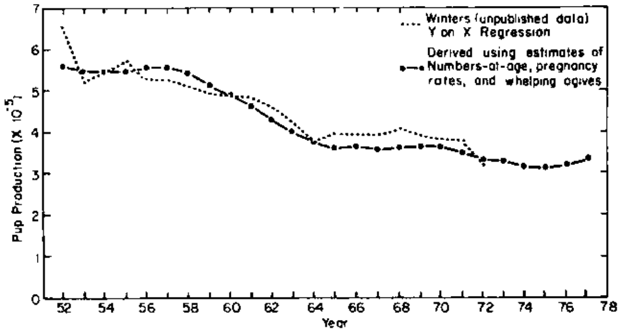

Fig. 3. Estimates of pup production in the Northwest Atlantic from sequential population analysis and from Winters (unpublished data) based on survivorship indices.

samples for 1947–51. The average age frequency for 1952–56 was used to provide age compositions for 1947–51 which were included in the analysis for one run to produce the required population estimate of age 1+ animals for 1947.

A word of caution should go with these sequential population estimates. This type of analysis uses all of the input data to estimate the required numbers and there are no degrees of freedom to estimate error. Confidence limits on the estimated pup productions used to adjust the exploitation rates are indicated in Table 2. The age sample on which the population structure is based comprised fewer than 1,500 animals and most of these were less than 6 years old. Exploitation rates on age 1+ animals are very low, and, even though the catch data are probably quite good, the resultant best estimates of numbers-at-age in the population are likely to have sizeable confidence limits. However, there is an overall consistency in the results, giving confidence to the estimates of total population and population trends.

TABLE 4. Assumed terminal exploitation rates at age 25, exploitation rates for age 1+ and 11+ animels derived from sequential population analysis, and ratios of age 25 to age 11+ exploitation rates for harp seals in the Northwest Atlantic.

		Average for		Ratio
Year	Age 25	Age 1+	Age 11+	(25/11+)
1952	0.025	0.058	0.066	0.378
1953	0.021	0.045	0.054	0.384
1954	0.014	0.041	0.038	0.384
1955	0.013	0.040	0.035	0.385
1956	0.009	0.026	0.023	0.383
1957	0.012	0.039	0.032	0.381
1958	0.022	0.076	0.059	0.378
1959	0.011	0.041	0.029	0.377
1960	0.015	0.060	0.039	0.373
1961	0.002	0.012	0.006	0.369
1962	0.010	0.049	0.028	0.366
1963	0.019	0.058	0.052	0.364
1964	0.025	0.069	0.069	0.367
1965	0.009	0.035	0.024	0.359
1966	0.017	0.055	0.048	0.359
1967	0.019	0.054	0.053	0.358
1968	0.014	0.040	0.040	0.357
1969	0.018	0.049	0.051	0.355
1970	0.015	0.041	0.043	0.354
1971	0.007	0.021	0.019	0.354
1972	0.006	0.017	0.016	0.353
1973	0.016	0.038	0.045	0.352
1974	0.012	0.032	0.033	0.351
1975	0.006	0.022	0.017	0.351
1976	0.004	0.017	0.011	0.350
1977	0.004	0.012	0.008	0.528

Density-dependent mortality in the first year

The estimation of pup production by cohort analysis (Lett and Benjaminsen, 1977) gave more erratic results than would be expected for a marine mammal population. They postulated that the variation may be attributable to a fluctuating natural mortality rate of pups which in some manner responds to exploitation.

The existence of density-dependent mortality was investigated, using the numbers of age 1 animals from the sequential population analysis and estimates of the number of pups from the application of the maturity ogive and pregnancy rate to the population estimates derived from the sequential population model. Escapement was determined by subtracting the catch from the estimates of pup abundance for the period 1950–76. The natural mortality of pups (M_o) was then obtained from the equation

$$M_o = ln(\mathrm{ESC}/N_1) \qquad (4)$$

where ESC is the escapement, and N_1 is the abundance at age 1 from the sequential population analysis. Due to high year to year variability, the estimates were averaged over 5-year periods as follows:

Period	Escapement ± 1SE	Mortality ± 1SE
1952–56	319.2 ± 30.0	0.48 ± 0.11
1957–61	344.2 ± 25.3	0.50 ± 0.14
1962–66	150.6 ± 20.5	0.07 ± 0.22
1967–71	137.8 ± 19.9	0.09 ± 0.09
1972–76	197.6 ± 10.6	−0.08 ± 0.05

It is clear from this analysis that there has been a significant decrease in natural mortality that seems to be related to escapement (Fig. 4). However, because of the way in which the points are spaced, it is impossible to determine the exact nature of the relationship. One hypothesis may be a continuous response, while another may imply a kind of step function. The response presented in Fig. 4 is a compromise between the two. Furthermore, it is interesting to note that the average of the natural mortality values in the above table (M = 0.2) is twice that of age 1+ seals. This is the exact level proposed by Lavigne *et al.* (MS 1976) for animals of age-group 0.

Are these estimates of natural mortality real or simply anomalies of the manner in which the data were

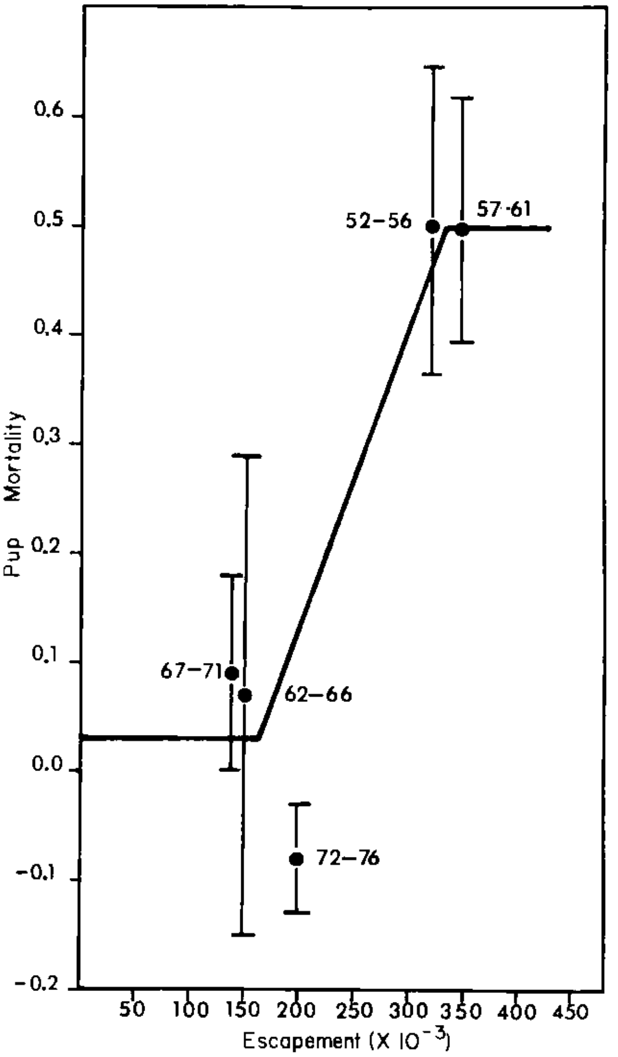

Fig. 4. Pup mortality as a function of escapement for the Northwest Atlantic harp seal population, 1952–76. (The limits indicated by vertical lines represent the mean ± 1 standard error.)

analyzed? In our opinion, this is a sound relationship. A continuous relationship exists only for values prior to 1962. The 1962 year-class was 15 years old in 1977, and there may be a problem with the initial estimation of numbers at age. This error could be the result of a severely biased sample of molting animals, since it is unlikely that errors in the sex ration or the maturity ogive would have much effect on the results. Furthermore, it is difficult to see how a consistent bias in sampling could result in such an abrupt change between the periods 1957-61 and 1962-66.

Density-dependent mortality in the first year of life has been shown for the grey seal, *Halichoerus grypus*, breeding at the Farne Islands (Bonner, 1975) and for the northern fur seal, *Callorhinus ursinus*, (Lander and Kajimuira, 1976). The most important cause of death in the young grey seal is starvation on shore. This occurs when the bond between the mother and her young is broken and the juveniles become separated from their food supply (Bonner, 1975). This mechanism cannot be hypothesized for harp seals, since the escapement occurs after the hunt for beaters which is long after the animals have weaned. Mortality in the northern fur seal has been related to their high density on land, resulting in increased incidence of hookworm. Apparently, some critically high level of density is necessary before the parasitic infection reaches epidemic levels (Lander and Kajimuira, 1976). The infection causes internal hemorrhaging, weakening and eventual death of the host. Furthermore, there is some speculation that weakened animals are less able to survive oceanic storms.

With virtually no knowledge of parasitic infection in harp seals, it is difficult to hypothesize the existence of a similar mechanism. The only reasonable hypothesis involves the food supply and the rigors of the first northerly migration. The 0-group seals feed mainly on euphausiids in the surface layer during their stay off northeastern Newfoundland and their subsequent migration to Greenland (Sergeant, 1973a; H. Fisher, personal communication). Before the northward migration begins, the seals form feeding aggregations. It is possible that the competition at this time for the limited food resource results in some seals being unfit to make the long migration northward. Sergeant (1973a) noted that very small juvenile seals do not attempt to migrate and therefore become separated from the major supplies of food. Lavigne *et al.* (MS 1976) observe that lean seals have a higher metabolic rate than fat seals. Thus, a density-dependent mechanism which results in a lean seal would have an enhanced effect on the animal's physical state, since more of its energy reserve would be required to maintain a constant body temperature and less could be used for the gathering of food, resulting eventually in death. Intense competition for food at the high levels of escapement prior to 1962 may have been the reason for the much higher mortality rates estimated for the early periods. Given the level of knowledge on this subject, there may be several equally plausible theories. In any case, a density-dependent relationship seems to exist and more research is required for its validation.

Density-dependent age of whelping

For female hapr seals, the current stage of maturity can be judged by examination of ovaries for the presence or absence of a new *corpus luteum*. This structure is obvious well before the time of implantation of the embryo, an event that is delayed several months in seals (Sergeant, 1973b). While the presence of a *corpus luteum* does not necessarily indicate a successful pregnancy, it indicates that maturation of a follicle has taken place. Øritsland (MS 1971) used the back-calculation of *corpus albicantia* as an indication of the age of sexual maturity. This technique can be misleading in that the small scars persist only for a few years, perhaps 3-4 years for harp seals (Sergeant, 1973b).

It is possible that the mean age of maturity has varied over the years, in addition to the standard deviation of the maturity ogive. Variation in the standard deviation was checked by standardizing all of the ogives to a mean age of zero and looking for inconsistencies in the rate of accumulation of mature animals within the population. Since all of the ogives superimposed one another, it was concluded that the standard deviation was not varying.

Cumulative normal distributions and arcsine transformations were used to linearize the data in different years. It was found, in accordance with Lett and Benjaminsen (1977), that the arcsine transformation, using a range between 0° and 90°, gave the best fit to the data:

$$ {}_tE_a = \text{sine}\ (31.34 + 19.91\ a) \qquad (5) $$

with $r^2 = 0.92$ and $F = 133.4$, where ${}_tE_a$ is the fraction whelping at age a in year t, r is the correlation coefficient, and F is the variance ratio.

The point of 50% maturity was interpolated from the various curves in different years and regressed against the age 1+ population sizes (POP_{t-n}) with different time lags to see which gave the best fit. The lag producing the highest correlation was 5 years (Fig. 5), and thus the functional regression developed to describe shifts in the mean age of whelping ($\bar{A}$) yielded

$$ \bar{A} = 3.875 + 9.126 \times 10^{-7}\ POP_{t-5} \qquad (6) $$

with $r^2 = 0.90$ and $F = 20.4$. Consequently, the proportion whelping at age a in year t was obtained from the relationship

$$ {}_tE_a = \text{sine}\ [31.34 + 19.91\ a - (3.875 + 9.125 \times 10^{-7}\ POP_{t-5})] \qquad (7) $$

Sergeant (1966, 1973b) first proposed that the mean age of maturity was density-dependent. Indeed, this phenomenon is known to occur in other marine and terrestrial mammals (Gambell, 1973; Markgren, 1969). Lett and Benjaminsen (1977) developed a mathematical relationship for harp seals. Laws (1956, 1959) noted that, in Phocidae, sexual maturity is attained at a constant proportion of the final or asymptotic body weight (about 87%) and that it is attained at an earlier age when growth is accelerated. If the growth rate of juvenile harp seals is density-dependent in a manner similar to the mortality rate, this sould provide the mechanism for density-dependent maturity. The 5-year lag is certainly consistent with Laws' observations.

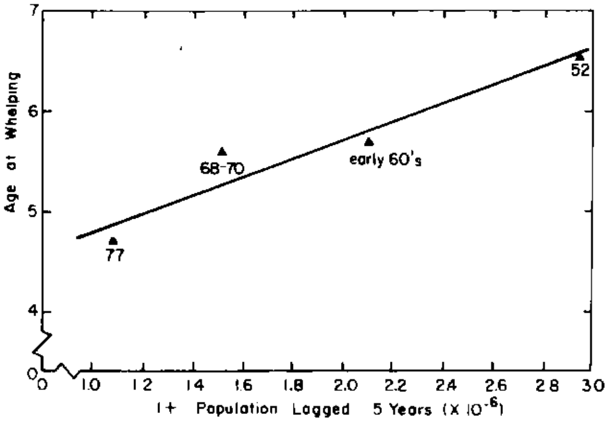

Fig. 5. Mean age at whelping as a function of age 1+ population size five years earlier, for the Northwest Atlantic harp seal population.

Density-dependent fertility rate

Density-dependent fertility was first noted by Lett and Benjaminsen (1977). All of the available data on the fertility rate found in the literature are presented in the following table:

Year	Estimate of fertility rate	Reference
	Front	
1953	89.0	Sergeant (1966)
1964-67	92.1	Øritsland (MS 1971)
1968	95.5	Sergeant (MS 1969)
1968-70	97.8	Sergeant (MS 1976a)
1976	95.4	Sergeant (MS 1976a)
	Gulf	
1951-54	86.0	Sergeant (1966)
1952	80.0	Fisher (1952)
1964	84.0	Sergeant (1966)
1965	90.0	Sergeant (1966)

The data are plotted against the age 2+ population size in Fig. 6, indicating a fairly clear density-dependent relationship. The data were plotted against the age 2+ population size because the younger animals remain segregated from the herd and may not compete for the available food resources. Data for the same year for both areas were combined and the following equation was derived using functional regression:

$$ PR_t = 102.297 - 7.3734 \times 10^{-6} \times {}_2POP_{t-1} \qquad (8) $$

with $r^2 = 0.69$ and $F = 6.58$, where PR_t is the pregnancy rate (%) in year t, t is the year in which the pups were

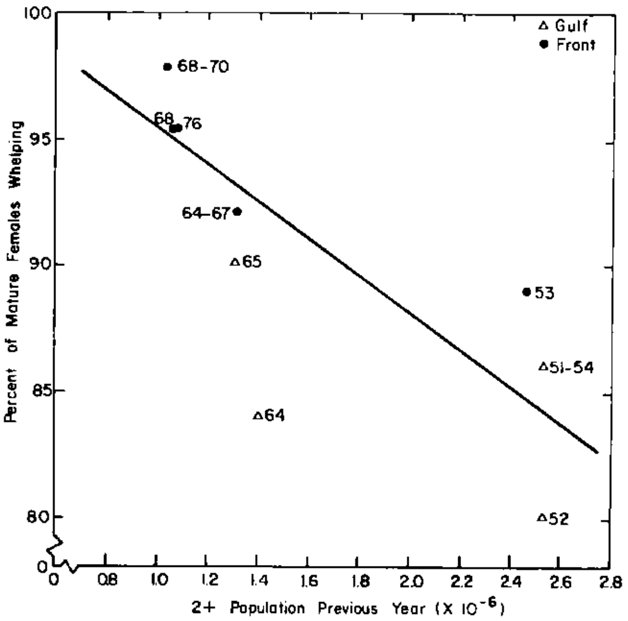

Fig. 6. Percentage of mature females whelping as a function of the age 2+ population size in the previous year, for the Northwest Atlantic harp seal population.

produced, and $_2POP_{t-1}$ is the age 2+ population in the preceding year (i.e. the year in which they became pregnant).

Variable fertility rates are well known in mammals and have been observed in at least three populations of whales (Gambell, 1973). Also, the unexploited population of Antarctic crabeater seals, *Lobodon carcinophagus,* which, like harp seals, have an unlimited extent of ice on which to whelp, and a low pregnancy rate of 0.76 (Øritsland, 1970). Markgren (1969) found that the ovulation rate in moose, *Alces alces*, was related to such factors as age, body size, nutrition and population density. Indeed, it is well known that fertility varies markedly in managed, utilized deer herds, *Odocoileus virginianus*. Nazarenko (1975) presents data on the White Sea stock of harp seals, indicating a fertility rate of only about 69%. The reason for the discrepancy between the White Sea and the Northwest Atlantic populations of harp seals is unclear.

Construction of the Simulation Model

The structure of the model is shown schematically in the Appendix. A detailed description follows from which one could construct the actual computer program. This program, which has evolved from the APL listing given by Lett and Benjaminsen (1977), allows the used to estimate the population as specified by sex and age for the Gulf and Front herds.

The starting population is separated into male and female components for the Front and Gulf. The ratio used to divide the Front and Gulf herds was 68:32 in all initializations. The sex ratios for both the Front and Gulf were initialized as listed in Table 5. The sex ratio of the large vessel catch at the Front followed the

TABLE 5. Proportional distribution of catch and the proportion of females as a function of age, as used in the simulation model of the Northwest Atlantic harp seal stock.

	Distribution of catch by age						Female sex ratio	
	Landsmen		Large vessels					
Age	Front	Gulf	Front	Gulf	Greenland	High Arctic	Initial	Vessel catch
1	0.120	0.034	0.300	0.034	0.306	0.131	0.50	0.47
2	0.100	0.081	0.134	0.081	0.185	0.160	0.50	0.47
3	0.090	0.122	0.080	0.122	0.125	0.212	0.50	0.41
4	0.090	0.108	0.060	0.106	0.084	0.116	0.50	0.36
5	0.080	0.093	0.050	0.093	0.058	0.083	0.50	0.31
6	0.070	0.089	0.040	0.089	0.042	0.062	0.50	0.27
7	0.060	0.079	0.040	0.079	0.031	0.046	0.50	0.24
8	0.050	0.066	0.030	0.066	0.024	0.037	0.51	0.21
9	0.050	0.050	0.030	0.050	0.018	0.029	0.51	0.19
10	0.040	0.047	0.030	0.047	0.015	0.023	0.51	0.17
11	0.040	0.039	0.020	0.039	0.013	0.018	0.51	0.16
12	0.030	0.035	0.020	0.035	0.011	0.015	0.52	0.15
13	0.030	0.023	0.020	0.023	0.010	0.013	0.52	0.15
14	0.020	0.022	0.020	0.022	0.009	0.010	0.53	0.15
15	0.020	0.022	0.020	0.022	0.008	0.008	0.53	0.15
16	0.020	0.013	0.020	0.013	0.007	0.007	0.56	0.15
17	0.020	0.015	0.020	0.015	0.007	0.006	0.59	0.15
18	0.010	0.014	0.010	0.014	0.007	0.005	0.59	0.15
19	0.010	0.008	0.010	0.008	0.008	0.004	0.62	0.15
20	0.010	0.019	0.010	0.019	0.008	0.003	0.57	0.15
21	0.010	0.007	0.010	0.007	0.006	0.003	0.63	0.15
22	0.010	0.005	0.010	0.005	0.006	0.003	0.68	0.15
23	0.010	0.005	0.010	0.005	0.006	0.002	0.74	0.15
24	0.005	0.003	0.005	0.003	0.005	0.002	0.69	0.15
25	0.005	0.003	0.001	0.003	0.005	0.000	0.81	0.15

distribution in the last column of Table 5 and that of the large vessel catch in the Gulf was assumed to be 50:50. These steps correspond to the block labelled "Initialize parameters" in the Appendix.

The age distributions of the catch are based on those reported in Lett and Benjaminsen (1977) except for the catches by landsmen and large vessels in the Gulf. These two distributions were compiled from data for the La Tabatiere fishery during 1952-60. The catch distributions used to decompose the input catch levels in all simulations are given in Table 5. The catches of age 1+ animals, except those for the large vessels, were simulated to be "stochastic", i.e. the user of the model has the option of allowing these catches to be drawn from a normal distribution with the mean given as input and the standard deviation given as a percentage of the mean. A coefficient of variation of 40% was chosen to approximate the data reported in Lett and Benjaminsen (1977). If only one run of the model is made, the catches are constrained to the means of the distributions. If two or more stochastic runs are made using a given set of catch leve inputs, the catches are chosen from their respective distributions and appropriate statistics are compiled. This option was introduced in the model to allow estimates based on mean values alone as well as those with associated variances. The normal distribution was simulated in the computer by using the Müller (1958) transformation on random numbers uniformly distributed between 0 and 1, as supplied by a FORTRAN subroutine. This transformation is

$$Z = -2\,ln(U_1)\cos(2\pi U_2) \qquad (9)$$

where U_1 and U_2 are "random" numbers. The distribution of Z has zero mean and unit standard deviation. The stochastic values are obtained by specifying the desired mean (m) and standard deviation (s) as follows:

$$Z' = m + sZ \qquad (10)$$

The catch by large vessels was modelled without a standard deviation, as this could be specified as a given catch for each of the Front and Gulf herd or as an exploitation rate (μ). Due to the short duration of the hunt, this rate was multiplied by the population entering the hunt to give a catch level. The μ was assumed to be constant over all age-groups of the age 1+ population so that the catch was proportional to the numbers-at-age. Also, only one value of μ was used in the simulations for both the Front and Gulf.

One complication exists with reference to mixing of the Gulf and Front herds during the period of exploitation, if quotas are based on area instead of total catch. Immature harp seals born in the Gulf have been found in the catch at the Front. On the basis of tag-return data (Sergeant, MS 1977), the probabilities of a Gulf-born animal being found at the Front are 0.79, 0.69 and 0.11 for age-groups 1, 2 and 3 respectively. This phenomenon was taken account of in the model by dividing the Gulf herd according to these probabilities, subtracting the catches by area, and then returning the surviving Gulf-born animals at the Front to their own herd for the remainder of the annual cycle.

In the simulation of the annual cycle (see Appendix), the input of a population size divided by herd and by sex establishes the catch by age, sex and herd. However, most of the seal hunt takes place after whelping. Consequently, the population size of age 2+ animals one year earlier is used to determine the pregnancy rate. If the density-dependence was not desired in a particular run, the pregnancy rate was set at 0.92 of the mature female population. If density-dependence was desired, the following relationship was used:

$$PREG = CP1 + CP2 \times {}_2POP_{t-1} \qquad (11)$$

where ${}_2POP_{t-1}$ is the age 2+ population lagged by 1 year. The values of CP1 and CP2 were determined to be 1.0293 and 7.373×10^{-6} respectively based on the best linear fit to the existing data (Equation 8). Also, for comparison, a "steeper" set of coefficients, CP1 = 1.05 and CP2 = 9.0×10^{-8} were used.

A linear relationship was also derived to relate the mean age of whelping (MAW) to the population size. Analysis of the data showed that a 5-year lag in the population produced the best agreement between the variables (Equation 6), and the following relationship was used:

$$MAW = CA1 + CA2 \times POP_{t-5} \qquad (12)$$

The values of CA1 and CA2 are entered with the starting population size at the beginning of the simulation. For the population size in 1977, the values were 3.875 and 9.126×10^{-7} respectively.

The mean age of whelping was not allowed to fall below 4.5 years, as there are no data to justify using a lower value. This corresponds to limiting the ogive≡s translation when the population size declines to 0.8 million animals. The ogive describing the probability of maturity with age is sinuousidal in shape and was modelled by the relationship

$$OGIVE = SIN[31.34 + 19.91(AGE-MAW)] \qquad (13)$$

which corresponds to Equation 5.

With the pregnancy rate and maturity ogive determined, the pup production was estimated by

$$\text{PUP} = \text{PREG} \times \text{OGIVE} \times \text{FEMALE} \times 1.06 \qquad (14)$$

The factor 1.06 was included to compensate for the number of females over age 25, as reported by Lett and Benjaminsen (1977). These equations are found in the block labelled "Pup production" in the Annual Cycle (see Appendix).

The previously determined catches are now subtracted from the population consisting of age 1+ animals and new born pups. A natural mortality of 0.1, treated as a stochastic variable with a standard deviation of 0.015, was then applied to the age 1+ population. Pup mortality was either set a 0.2 or determined as a function of the escapement (number of pups surviving the hunt). The function relating pup mortality to escapement was

$$\bar{M}_{pup} = -0.3507 + 2.35 \times 10^{-6} \times \text{ESC (best estimate)} \qquad (15)$$

or $$\bar{M}_{pup} = -0.764 + 3.925 \times 10^{-6} \times \text{ESC (steeper estimate)}$$

The pup mortality was constrained to a range of 0.03–0.50, as in Fig. 4, and was assumed to have a standard deviation of 0.03. After the mortalities were determined, the population was reduced by using the simple exponential model:

$$\text{PUP} \leftarrow \text{PUP} \times \text{EXP}\,(-M_{pup}) \qquad (16)$$

and $$\text{POP}_{1+} \leftarrow \text{POP}_{1+} \times \text{EXP}(-M_{1+}) \qquad (17)$$

where the arrow signifies "replaced by". The age structure of the population was next determined with the surviving pups replacing age-group 1, age-group 1 replacing age-group 2, etc., thus finishing the annual cycle (see "Natural Mortality" block in the Appendix). The cycle can be repeated to simulate the population in the following year. The actual simulation program was limited to 50 years for a given set of parameters.

Statistics on breeding population, new-born pups, pups surviving to age 1, population size, and the catches of adults and pups were compiled for both the Front and Gulf for each year. When only one stochastic run was made, the means of all stochastic variables were used in the equations. When more than one run was specified, the program was run for the required number of years and then restarted from the initial step using new values drawn for the stochastic variables. This process was repeated for the specified number of runs and the relevant statistics compiled for each run, from which the means and standard deviations for the breeding population, the total population, and the catches of pups and adults were calculated.

The model provided for the pregnancy rate, the whelping ogive and pup mortality to operate in a density-dependent manner or be set at constant values. In order to demonstrate the effects of these density-dependent factors, projections were made with one, two or three operating. (Fig. 7, 8 and 9).

Population sizes as a function of time were projected with the hunt limited to the high Arctic and Greenland components. These variables were set at the mean values presented in Lett and Benjaminsen (1977) and were retained in all projections, since they are presumed to be outside the control of management options but still must be taken into consideration.

Sustainable yields were estimated by projecting the 1977 population ahead for 50 years under varying hunting mortalities. Such estimates of catch are not strictly sustainable yields because the projected population and catch after 50 years may be still slowly changing, whereas sustainable yields imply equilibria, but the discrepancies should be small and should decrease as the projected population approaches the initial population size. For example, the maximum of the curve (Fig. 10) is not far removed from the starting population of 1.39 million, and the area of concern for management is therefore not affected by this bias. Six sets of results were compiled according to the following schedule:

Set	Whelping ogive	Pregnancy rate	Pup mortality	Comment
1	variable	variable	variable	"best" estimates
2	variable	variable	variable (steep)	for comparison with
3	variable	variable (steep)	variable	"best" estimates
4	variable	constant	constant	to show effects
5	variable	variable (steep)	constant	of removing
6	variable	variable	constant	feedback loops

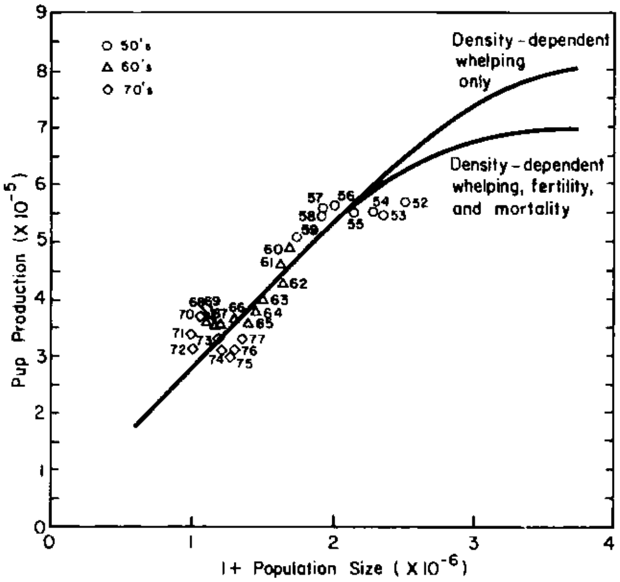

Fig. 7. Pup production as a function of age 1+ population size for the Northwest Atlantic harp seal stock, 1952-77.

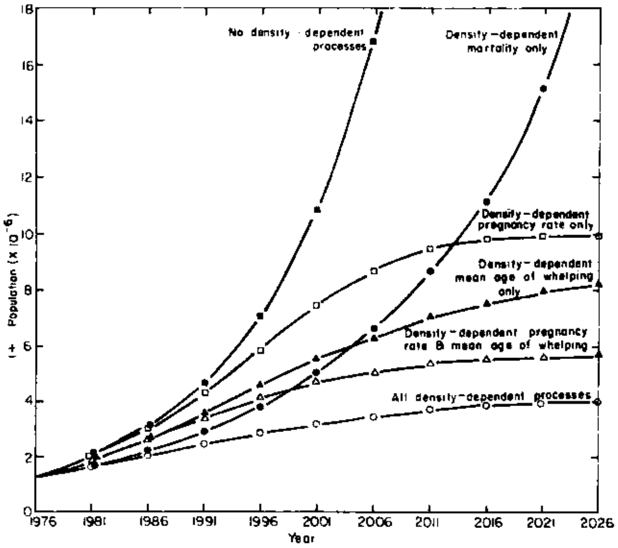

Fig. 8. Projected population sizes of harp seals resulting from various combinations of density-dependent controls, with hunting mortality restricted to aboriginal catches in the Arctic and at West Greenland.

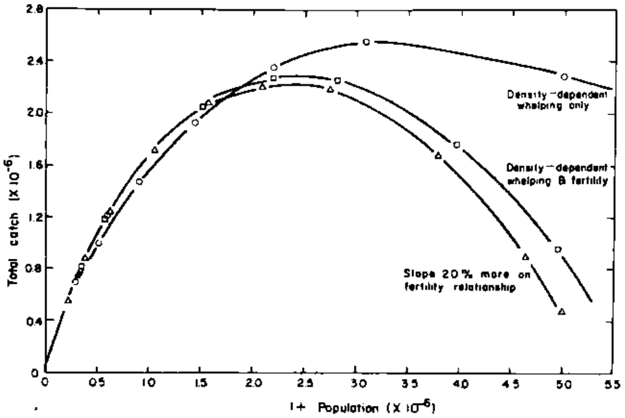

Fig. 9. Sustainable yield estimates for harp seals resulting from the use of one and two density-dependent controls, with pup mortality set at 0.2 in each case. For the simulation with one density-dependent control (circles), the pregnancy rate was held constant at 0.92.

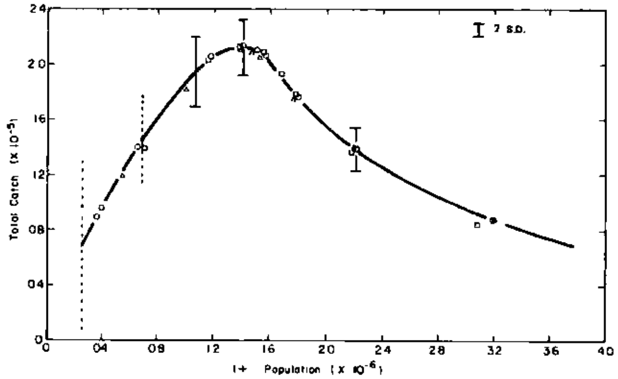

Fig. 10. Sustainable yield estimates for harp seals resulting from the use of three density-dependent controls. Circles represent the results from using the "best" estimates of coefficients in the equations for mean age of whelping, pregnancy rate, and pup mortality. Triangles and squares represent steeper pup mortality and pregnancy rate relationships respectively. Two standard deviations are indicated for some points by vertical lines; the dashed lines are estimates for points where the population sometimes collapsed.

Each data point in Fig. 8, 9 and 10 is based upon one run with the stochastic variables fixed at their mean values, unless error bars are present. The points with error bars represent the means of 10 runs with the stochastic variables drawn from their respective distributions. The exploitation rates used in the projections of sustainable yield were required to yield catches of pups and age 1+ animals in the ration of 80:20. For practical consideration, if the proportion of pups in the catch fell in the range of 0.195–0.205, the simulation was considered to be adequate. This level of performance generally required less than three trials for a given level of exploitation, once the user became familiar with the model.

Results and Discussion

Sequestial population analysis

The present sequential population analysis shows that the population of age 1+ seals declined from 2.5 million in 1952 to 1.0 million in 1972 and increased to

1.3 million in 1977 (Table 3). Estimates by Lett and Benjaminsen (1977) indicate that the stock declined from 2.3 million in 1952 to a low of 1.0 million in 1968 and increased to 1.2 million in 1975. The analysis in Lett and Benjaminsen (1977) is a cohort analysis utilizing data for the years 1952 to 1975. Starting exploitation rates for 25-year-olds in 1975 were derived by averaging rates for ages 10-20 in 1973 and 1974, and pup mortality was assumed to be the same as the adult mortality at M = 0.114. Despite these differences from the present analysis, it is interesting that the age 1+ population estimates from the cohort analysis agree so well with the present results.

Pup production, estimated from the sequential population analysis, declined from 570,000 in 1952 to 310,000 in 1975 and increased to 330,000 in 1977 (Fig. 3). These estimates are very close to those of Winters (unpublished data) for 1953 to 1972. The cohort analysis of Lett and Benjaminsen (1977) gave estimates of pup production that varied considerably from those shown in Fig. 3, due to the manner in which the starting values for hunting mortality were derived. Overall, however, these do show the same general trend of a decline from high values in the 1950's to a low of 310,000 in 1973. Re-estimation of pup production from the cohort analysis and other data gave values of 290,000 in 1972, 310,000 in 1975 and 320,000 in 1977. Although the minimum occurs a little earlier in the cohort analysis than in the present analysis, the same trend is apparent toward an increase in the most recent years.

Various methods have been used to estimate pup production in the Gulf of St. Lawrence. Sergeant (MS 1975), using survivorship indices, estimated production at 120,000 in 1958 and 85,000 in 1967. Using catch and effort data, Lett *et al.* (MS 1977) estimated that production averaged about 98,000 pups during 1964-71, a value which seems reasonable, since the total kill of pups in the Gulf was 72,000 in 1971. Sergeant (MS 1975) indicated that this figure was probably close to the total production, as the ships could not complete their quotas in the year and seals could not be found after the hunt for branding. However, there was some escapement, because beaters were taken by landsmen of western Newfoundland during their northward migration through the Strait of Belle Isle. According to Lett *et al.* (MS 1977), the total production in the Gulf in 1971 was about 90,000 pups. They also estimated production at 89,000 animals in 1975, in contrast to Lavigne's (MS 1975) minimum estimate of 46,000, based on aerial photography. Lett *et al.* (MS 1977) estimated 1977 production in the Gulf at 93,000 pups. Adding this figure to the 1977 estimate of 210,000 pups at the Front (Lavigne *et al.*, MS 1977) gives a minimum estimate of overall production in 1977 of 303,000 pups, a figure only slightly below the estimates derived by cohort analysis and sequential population analysis.

Comparison of the simulation with other models

The simulation model can be operated with up to three density-dependent controls. This compares with the model described by Capstick *et al.* (MS 1976) which has only density-dependent maturity and with the model of Lett and Benjaminsen (1977) which has density-dependent maturity and pregnancy. The effect of increasing the number of feedback controls is generally to stabilize the model. This stability is reflected in the ability of the modelled system to respond to changes either in the environment or in fishing effort. Also, the incorporation of several feedbacks reduces the effect of an error in the estimation of a particular parameter. The sensitivity of the system is a measure of the effect that a change in an input parameter would have on output results, e. g. population size or sustainable yield. The sensitivity of individual input parameters tends to be reduced in models with several feedback controls. Mohn (MS 1977) demonstrated this in comparing the sensitivity of natural mortality in models with one and two feedback controls.

Qualitatively, it is desirable to consider the effect of including all three feedbacks in our model, because its sensitivity for a given parameter is generally reduced as more parameters are involved. For example, the response to increasing the pup catch would be a change in the mean age of whelping, an increase in the pregnancy rate and a decrease in pup mortality, thus making the final projected population size less sensistive to the change in pup kill than would be the case in a simpler model without density-dependent controls. Therefore, if the available data indicate the presence of density-dependent factors, it is generaly beneficial to include all such factors in the simulation. However, because the total uncertainty in the results projected by the model is a function of the uncertainties associated with the individual parameters, density-dependent controls should not be included when the data do not warrant it.

Relationship between pup production and age 1+ population

Catches of young harp seals have been higher than 600,000, and pup productions in excess of the 1952 level were necessary to sustain the earlier levels of catch (Chafe *et al.*, 1923). Therefore, recruitment curves were simulated under a number of assumptions to investigate the validity of certain density-dependent mechanisms (Fig. 7). When all three factors (age of whelping, pregnancy rate and mortality rate) are related to population density, the whelping rate decreases to 0.16 at a population size of 4.3 million. The natural mortality of pups is 0.5 at this population size, which gives a recruitment rate of

$$R = 0.16 \times \exp(-0.5) - 0.10$$

which balances the natural mortality of the age 1+ population.

When the fertility rate is held at 0.92 (a long-term average value), the natural mortality of pups is held at 0.2 and the maturity ogive is allowed to vary, the resultant recruitment curve diverges from the first at an age 1+ population size of 2.2 million (Fig. 7) and pup production increases to more than 800,000 at an age 1+ population of 3.75 million. At this level fo stock size, the whelping rate is 0.20 compared with a value of 0.18 for the simulation with all three density-dependent factors operating. Thus, a mechanism that regulates the mortality of pups may have a significant effect on the rate of recruitment to the stock and on the maximum size that the population can achieve. This study indicates that pups may represent between 0.16 and 0.22 of the total population compared with Sergeant's (MS 1975) statement that 0.20 to 0.25 of the total population are pups.

It is important to note that the stock-recruitment curves (Fig. 7) do not have descending right limbs. Lett and Benjaminsen (1977) state that a recruitment curve for a stock as undynamic as harp seals cannot have a descending right limb. Thus recruitment does not appear to follow either the Beverton and Holt (1957) or the Ricker (1954) recruitment curve, although Allen (1975) points out that fitting either curve would not greatly affect management decisions over a wide range of stock sizes. Allen (1973) shows a similar recruitment pattern for fin whales (*Balaenoptera physalus*), although it is not clear from his raw data whether the shape is due to a changing population structure or a change in maturity. In general, a truncated sinusoidal function seems to fit the data from the sequential population analysis quite well (Fig. 7), the autocorrelative nature of the points being a result of a fluctuating population structure. However, over the time series of biological sampling (1952-77), the population has not been large enough to indicate which of the two recruitment curves is superior.

Maximum population size

Sergeant (MS 1975) has indicated that the population in 1952 may have been near the maximum population size on account of the poor condition of the molting adults. The present study indicates that, no matter what set of assumptions are used, the population of age 1+ seals achieves a maximum of at least 4 million, compared with 2.5 million in 1952 from the sequential population analysis. However, the assumptions about the factors controlling the dynamics of the population severely affect estimates of the virgin stock size, as indicated by the 50-year projections (Fig. 8). When no density-dependent factors are operating, the population increases continuously at a rate of 9% per year. Also, density-dependent pup mortality alone does not seem to constrain the population which continues to grow at a rate of 4% per year.

The growth of the population becomes asymptotic when the density-dependent pregnancy rate or the density-dependent age of whelping are operating independently (Fig. 8). Under the assumption of density-dependent pregnancy rate, the maximum population size is about 10 million, which is somewhat higher than the estimate of Lett and Benjaminsen (1977), but it depends also on assumptions concerning mean age of whelping and mortality in the first year. Density-dependent age of whelping alone constrained the population to about 8 million animals. It can be concluded therefore that, of the three density-dependent relationships used in the simulation, that influencing the age of whelping has the greatest control over fluctuations in population size.

When both density-dependent pregnancy rate and age of whelping operate together, the maximum population size is projected to be about 5.5 million (Fig. 8). Lett and Benjaminsen (1977) found that, under a similar set of assumptions, the population size never exceeded 4.1 million. However, in their model the aboriginal hunt in the Arctic and the landsmen hunt were both allowed to continue (but no large vessel hunting activity), whereas in the present model no hunting activity is allowed except for a small amount of hunting in the Arctic which is considered by some researches (Capstick *et al.* MS 1976) as a part of natural mortality. With all three density-dependent processes operating, the projected maximum population size is 4.2 million seals (Fig. 8).

Production curves and density-dependence

The fitting of general production models to data, whether it be catch as a function of average exploitation rate or as a function of total population size from sequential population analysis, gives poor statistical relationship. Indeed, our efforts resulted in a coefficient of determination of only 4%. Using the simulation model with density-dependent mechanisms operating, four sets of data were generated as an experiment, each consisting of 50 ordered pairs of age 1+ population size and total catch. The ratio of pups to adults was maintained at 80:20. The exploitation rate was assumed to follow a sine function with associated variance such that

$$\mu = [\sin(\pi/50\ t) + \delta]\ C_1 + C_2 \quad (18)$$

where δ is a random normal variate with zero mean and standard deviation of 0.1, and where C_1 and C_2 were chosen so that μ for pups oscillated between 0.1 and 0.55 (actually constrained between zero and 0.6). A second pair of C_1 and C_2 yielded μ for age 1+ animals between 0.004 and 0.036. The data were fitted using Gulland's (1961) technique with 5-year running averages. The maximum sustainable yield (MSY) was 196,000 seals at a population size of 1.71 million for the first 50 years of data. The addition of another 50 points yielded an MSY of 179,000 at a population size of 1.61 million animals. For this set of conditions in the complete model, the MSY is 215,000 for a corresponding population size of 1.4 million (Fig. 10). This constitutes at least a 9% error in the estimation of the MSY and an 18% error in the corresponding population size.

When only the density-dependent mean age of whelping was included in the simulation, Gulland's (1961) model could not be fitted to the first 50 years of data because the slope of the autocorrelative function of catch per unit population against population size was positive. By adding another 50 points, the MSY was determined to be 250,000 for a population size of 3.4 million. The corresponding "best" values were 255,000 and 3.1 million (Fig. 9). This study, although reliant on the initial assumptions, indicates that fitting production models can lead to serious errors, especially in the stock size corresponding to the MSY.

The degree of density-dependence has a profound effect on the shape of the curves and the determination of MSY, as indicated by the use of two density-dependent factors (mean age of whelping and fertility rate) in the simulation (Fig. 9) in contrast to allowing only the mean age of whelping to vary. The use of a fertility rate, which was 20% greater than the "best" estimate but still within the range of possibilities (Fig. 6), did not have much effect on the MSY which only decreased from 230,000 to 225,000. Higher fertility rates than those occurring on the average (0.92) would tend to increase the yield.

Lett and Benjaminsen (1977) indicated that the MSY is about 240,000 animals for a population size of about 1.6 million, while a recent update of the model (Lett *et al.*, MS 1977) indicated that the MSY is 220,000 for a population size of about 1.5 million. The basic difference between the two models is that a natural mortality coefficient of 0.114 was used in the former and 0.10 in the latter. Thus a 12% decrease in natural mortality rate leads to a decrease in the MSY estimate from 240,000 to 220,000 animals and in the associated population size. The results from the simulation model, with natural mortality of pups set at 0.2, indicate an MSY of 230,000 animals for a population size of 2.5 million (Fig. 9). In comparing the results of the three models, it must be considered that, when an assumption changes thus altering fundamental values such as numbers-at-age, all of the other variables in the model must change accordingly. Thus some of the discrepancies in MSY and population size are due to changes in the rates at which the mean age of whelping and the fertility respond to population size, or in general terms the degree of density-dependence.

When all three density-dependent factors were allowed to vary, the MSY decreased slightly to 215,000 animals but the associated population size declined greatly to 1.4 million (Fig. 10). The shape of the curve is due primarily to the hypothesized relationship between escapement and pup mortality (Fig. 4). At low stock sizes, the escapement is low and the mortality rate for pups is less than 0.1. At this low mortality rate, an increase in stock size results in a rapid rise in the production curve toward the MSY level. However, with the increase in natural mortality to its maximum level (0.5), the right limb of the curve declines rapidly at first, but the rate of decline decreases with increasing population once the escapement becomes greater than 300,000 animals.

In the general area of the MSY (Fig. 10), the populations size may vary from 1.0 million to 1.8 million while the sustainable yield varies only from 180,000 to 215,000. It is therefore difficult to specify a stock size that corresponds to an MSY as a viable management objective. The question then is how should the harp seal stock be managed in view of this kind of variability and uncertainty in the data.

The problems of environmental variability, in relation to general production models, in particular the Schaefer (1954) model, were discussed by Doubleday (1976) and Sissenwine (1977). Independently, Beddington and May (1977) also considered the problems of harvesting populations in a randomly fluctuating environment. Lett and Benjaminsen (1977) commented on the biological basis for an increase in the variability of the catch associated with a decrease in stock size. In the present model, a number of factors contribute to the overall variance, among them being uncertainties associated with natural mortality, with the uncontrolled aboriginal hunt in the Arctic and the hunt by landsmen of Newfoundland and Quebec. Although the incorporation of density-dependent mechanisms would be expected to stabilize a system, this may be offset to a degree by the uncertainty associated with the parameters used.

Density-dependence and critical stock size

Doubleday (1976) and Beddington and May (1977) indicated that, if the size of the stock is below the level corresponding to the MSY, it is more likely to collapse than one above that level. Furthermore, they indicate that it is better to harvest at a constant exploitation rate than at a constant quota level since the latter may cause the stock to fall below the sustainable yield level and not recover. For a harp seal population less than 800,000 animals, harvesting at a constant exploitation could lead to a collapse in the stock through natural fluctuations (Fig. 10).

The critical stock size for harp seal is the level at which certain density-dependent factors cease to operate. Most density-dependent factors are the result of varying amounts of surplus energy affecting the physiology of the animals. If a population can gather, eat and digest no more food than is now being utilized, the associated density-dependent factors can no longer have any effect on the population dynamics. For harp seals, the minimum age of maturity is about 4.5 years and a pregnancy rate greater than 0.98 has never been observed. Both biological limits are reached for a population size of about 800,000 animals, and any factors leading to lower population sizes (e. g. exploitation, disease, recruitment failure, inadequate food supply, etc.) cannot be compensated for. On the basis of the present analysis, this figure may be considered as the critical stock size.

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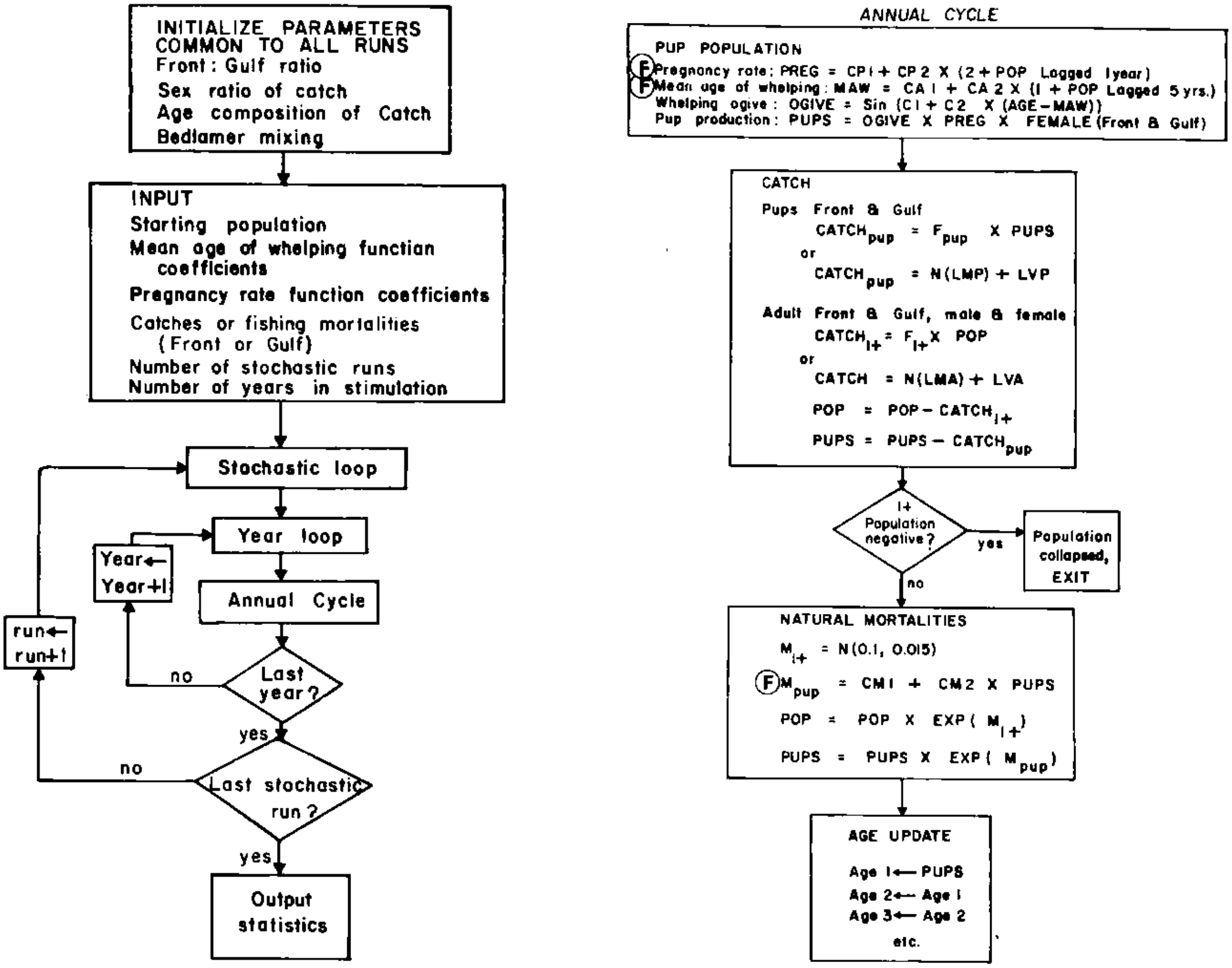
APPENDIX

Flow chart of the Northwest Atlantic Harp Seal Production Model and Details of its Annual Cycle.



Ⓕ	Feedback Controls
POP	1+ Population
PREG	Pregnancy rate – proportion of mature females that become pregnant
CP 1	Constant term in pregnancy rate function
CP 2	Linear term in pregnancy rate function
MAW	Mean age of whelping
CA 1	Constant term in mean age of whelping function
CA 2	Linear term in mean age of whelping function
OGIVE	Whelping ogive – proportion of females of a particular age that can potentially whelp
Sin	Sine function – argument constrained between 0° and 90 °
C 1	Constant term in whelping ogive function
C 2	Linear term in whelping ogive function
AGE	Vector of ages
PUPS	Number of pups produced
FEMALE	Vector of number of females of each age
$CATCH_{pup}$	Pup catch – separate values for Front and Gulf
F_{pup}	Fishing mortality rate on pups

N (a,b)	A draw from a normal distribution with mean 'a' and standard deviation 'b'
LMP	Mean and standard deviation of landsman pup catch – separate values for Front and Gulf
LVP	Large vessel pup catch – separate values for Front and Gulf
$CATCH_{1+}$	Adult catch – separate values for male and female, Front and Gulf
F_{1+}	Fishing mortality rate on adults
LMA	Mean and standard deviation of landsman adult catch – separate values for male and female, Front and Gulf
LVA	Large vessel adult catch – separate values for male and female, Front and Gulf
M_{1+}	Natural mortality rate on adults
M_{pup}	Natural mortality rate on pups
CM 1	Constant term in pup mortality function
CM 2	Linear term in pup mortality function
EXP	Exponential function

Instructions to Authors for the Preparation of Manuscripts Intended for Publication in the ICNAF Research Bulletin and Selected Papers

Text

a) Manuscript should be type-written, *double-spaced*, and on one side only of good quality white bond paper, size 8½ × 11 inches (220 × 280 mm).

b) Leave all margins 1 inch (25 mm) to 1½ inches (38 mm) for editorial marks and queries.

c) Prepare and submit the original and one copy of the text and two sets of illustrations.

d) Number all pages of the manuscript consecutively with Arabic numerals in the centre of the top margin space.

e) Start a new page for each of the following sections with appropriate headings and sub-headings: (1) title, name and address of author, list of contents (if applicable); (2) abstract of the paper; (3) text; (4) references to literature; (5) tables; (6) legends for figures and (7) figures.

f) Please *double-space everything* — Text, quotations, footnotes, tables and table headings, legends, references to literature, and use even greater spacing where helpful (particularly around equations and formulate).

g) Wherever practical the text should be subheaded into Abstract, Introduction, Materials and Methods, Results, Discussion and Acknowledgements. If authors wish to provide a summary of the conclusions, it should follow the Discussion.

h) All measurements, linear, weight, and time, should be given in numerals (not words) in the metric system. The Celsius scale should be used as a standard. When other units of measure are preferred, authors should include equivalents in metric units.

i) Footnotes should be avoided as far as possible, but if necessary they must be numbered consecutively in the text and typed under a horizontal line at the bottom of the page concerned.

j) Only those words to be printed in italics should be underlined.

Abstract

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.

Tables

a) Tables should be carefully constructed so that the data presented may be easily understood

b) Tables should be set out on separate sheets following the references.

c) Position of the tables in the text should be indicated clearly.

d) Each table should be provided with a descriptive heading which, together with the column headings, makes the table intelligble without reference to the text.

e) Tables should be numbered consecutively with Arabic numerals, e.g. Table 1, 2, 3, etc.

Figures

a) All illustrations, whether black-and-white drawings, graphs, photographs, or tone drawings, are to be considered as figures.

b) Each figure should be mentioned and described in the text.

c) A legend should be provided for each figure; the legends should all be typed together on a separate sheet or sheets attached to the manuscript following the tables.

d) Figures should be numbered consecutively with Arabic numerals, as Fig. 1, 2, 3, etc.

e) Figures should be set out on sheets preferably the same size as the text pages and in any case should not require a printer's reduction to less than one-third. Small figures can be arranged in groups on sheets the same size as the text pages.

f) For guidance in preparing figures, the size of the printed area of the page is 21 × 17 cm. The publications have a two-column format, each column 8 cm wide.

g) Photographs presented as figures should be high contrast, glossy prints, about 5 × 7 inches (125 × 175 mm) in size and should be shipped flat protected by stout cardboard.

h) Each illustration should be identified by marking the figure number and the author's name on the back lightly in soft pencil.

(over)

Bibliographic Style

a) References to literature in the text should be by the author-date system, for example

It was reported that (Collins, 1960) the...;
In examining the situation, Rossini (1959) felt that...

Where more than one paper by the same author(s) have appeared in one year, reference should be given as follows:

Osborne and Mendel (1914a); Osborne and Mendal (1914b)
or Osborne and Mendel (1914a and b); (Barnet and Robinson, 1942; King and Pierce 1943a, 1954)

Reference to material not yet submitted for publication should be written into the text e.g. "Harvey, in an unpublished manuscript,..." or "Harvey, in a letter,..."

b) All references cited by the author-name system in the text should be listed alphabetically by the surname of the first *author* at the end of the paper. *Year* of publication follows the authorship. Then give the full *title* of the paper. This should be followed by the abbreviated name of the *periodical* with the *volume* and *pages* in Arabic numbers (e.g.:2: 120-136). For abbreviations of periodicals follow the "Word List of Scientific Periodicals"[1]. An issue, number supplement or other part within a volume is shown in parentheses only when paged independently (e.g.:2(4):1-56; 34 (Suppl. 2):1-26). Any special Series (Ser 3, III or C) precedes the volume number. In *book citations* after the title, there appears the edition, the publisher's name, place of publication, and the number of pages if one volume, but the number of volumes if more. Reference to material submitted but not yet published should be referred to in the list of references as "in press" or "Submitted for publication" followed by the date of submission.

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[1] The following abbreviations *(in italics)* should be used when citing ICNAF publications and documents:

(ICNAF Res. Bull.) International Commission for the Northwest Atlantic Fisheries Research Bulletin
(ICNAF Sel. Papers) International Commission for the Northwest Atlantic Fisheries Selected Papers
(ICNAF Stat. Bull.) International Commission for the Northwest Atlantic Fisheries Statistical Bulletin
(ICNAF Redbook) International Commission for the Northwest Atlantic Fisheries Redbook
(ICNAF Annu. Rept.) International Commission for the Northwest Atlantic Fisheries Annual Report
(ICNAF Samp. Yearb.) International Commission for the Northwest Atlantic Fisheries Sampling Yearbook
(ICNAF Spec. Publ.) International Commission for the Northwest Atlantic Fisheries Special Publication
(ICNAF Meet. Proc.) International Commission for the Northwest Atlantic Fisheries Meeting Proceedings
(ICNAF List Fish. Vessels) International Commission for the Northwest Atlantic Fisheries List of Fishing Vessels
(ICNAF Res. Doc.) International Commission for the Northwest Atlantic Fisheries Research Document
(ICNAF Sum. Doc.) International Commission for the Northwest Atlantic Fisheries Summary Document
(ICNAF Com. Doc.) International Commission for the Northwest Atlantic Fisheries Commissioner Document