

International Commission for



the Northwest Atlantic Fisheries

Serial No. 3430
(D.c.3)

ICNAF Res.Doc. 75/2

ANNUAL MEETING - JUNE 1975

Review of capelin ecology and estimation of surplus yield from predator dynamics¹

by

G.H. Winters
Fisheries and Marine Service, Environment Canada
Biological Station, St. John's, Newfoundland, Canada

Introduction

Initial consideration of an appropriate TAC for capelin in Subareas 2-3 was undertaken by the Assessments Subcommittee of ICNAF at the 1973 Annual Meeting. Information presented to the Subcommittee at that time indicated that the surplus production of capelin was substantial and that potential catches in the order of 750,000 m. tons might be achieved. In view, however, of the paucity of data available on specific parameters relevant to accurate estimation of a TAC, and the critical role played by capelin in the marine ecosystem, the Assessments Scientists recommended a pre-emptive TAC of 250,000 m. tons for 1974 which was to be incremented annually according to the rate at which new information allowed the full potential of the resource to be assessed. National allocation and a minimum stock partition of the 1974 TAC were decided at the 1974 Mid-term Meeting held in Rome, January, 1974. At the 1974 Annual Meeting the Assessments Subcommittee considered new information presented by Canadian scientists which indicated that the greatest long-term yield of capelin would be achieved by an intensive fishery on mature capelin during the spawning season. Such a fishery could be permitted to remove all except that fraction of the spawning stock necessary for assurance of continued adequate recruitment. The Subcommittee therefore concluded that the appropriate next adjustment of the TAC for 1975 could be 500,000 m. tons which 1) should be maintained for at least 3 years to monitor the effect of the fishery on the resource, 2) should be restricted to mature capelin approaching and during the spawning season, 3) should be

¹ Presented to the Sixth Special Commission Meeting, January 1975, Bergen, Norway as Res.Doc. 75/2.

accompanied by intensified research efforts by countries participating in the fishery. Although recognizing the development of a new fishery in Division 3L the Subcommittee did not recommend a separate TAC for that fishery due to lack of appropriate stock discrimination data. In any event the management regime proposed by STACRES was not acceptable to all members of the Commission with the result that consideration of the magnitude, partitioning and allocation of the 1975 TAC for capelin was deferred to this meeting.

It is unlikely that a significant amount of new information on capelin will have become available in the interim between the 1974 Annual Meeting and this meeting. The author therefore considers it a useful exercise to review some pertinent aspects of capelin ecology in the Northwest Atlantic area and to attempt to provide an approximate estimate of excess yield of capelin from a crude deterministic model of predator dynamics.

Trends in recent landings

Capelin landings by ICNAF subdivisions for the period 1970-73 are shown in Table 1. Commercial exploitation of offshore capelin began in 1971 when the Soviets reported to ICNAF that their vessels had caught 750 m. tons of capelin on the Southeast Shoal of Grand Bank (3N). Landings increased substantially from less than 3000 m. tons in 1971 to 70,150 m. tons in 1972, the bulk of the catch being made by Soviet trawlers prosecuting a fall fishery in 2J-3K. A further substantial increase in landings to nearly 270,000 m. tons occurred in 1973, nearly half of which was derived from a summer fishery on spawning capelin on the Southeast Shoal, the remainder being taken from a fall fishery in 2J-3K. In 1974 capelin catches in Subareas 2-3 came under ICNAF quota regulations with the larger bulk of the TAC being allocated to the southern area (3LNOPa). During April-May, 1974, a new fishery was developed by Soviet trawlers off the eastern side of the Avalon Peninsula (Fig. 1) in 3L and a substantial portion of the 148,000 m. ton TAC was taken prior to the normal fishery in June-July on the Southeast Shoal.

Table 1. Landings of capelin by ICNAF Subdivision for the period 1970-73.

ICNAF Subdiv.	Year				
	1970	1971	1972	1973	1974
2GHJ	-	-	17838	59838	} 110000
3K	426	242	27785	76584	
3L	2266	870	1241	3875	} 148000
3N	-	750	16794	120501	
3O	-	-	3970	6374	
3Pa	307	999	2522	1356	
Total	2999	2861	70150	268528	258000

Growth and age composition

Capelin exhibit sexual dimorphism in size, males becoming increasingly larger than females up to the age of maturity after which growth differences are maintained (Templeman 1948; Pitt 1958; Winters 1974a). Spawning schools are normally dominated by 3 and 4 year olds although there are considerable annual variations in growth and age composition (Winters and Campbell 1974). For Grand Bank capelin Winters and Campbell (1974) found significant positive correlations between temperature and size-at-age and interpreted fluctuations in the relative abundance of 3 and 4 year olds as reflecting growth-induced variations in maturation rate rather than variations in survival rate. In this regard the consistent decline in water temperatures in the Northwest Atlantic area since the early 1950's (Rodewald 1972) has resulted in a decrease in growth rate and an increase in average age of mature capelin at least for the Grand Bank area (Winters and Campbell 1974). This trend is particularly evident in the 1970's as a result of the intensification of the cooling trend since 1971 (Table 2, below):

Table 2. Mean age of mature male and female capelin from Grand Bank, 1967-74.

Year	Mean age (years)		
	Males	Females	Combined
1967	3.4	3.7	3.5
1968	3.5	3.9	3.7
1969	3.7	3.7	3.7
1970	3.3	3.8	3.5
1971	3.4	3.3	3.4
1972	3.6	3.7	3.7
1973	3.9	3.9	3.9
1974	3.9	4.2	4.0

There is a general north-south cline in the growth of capelin in Subareas 2-3 (Winters 1974a) (Fig. 2) - capelin from Grand Bank and southern Newfoundland (3LNOPs) have a similar growth pattern and represent fish with a fast growth rate and large average size at age, particularly in fish less than 5 years old; Labrador (2J) capelin are characterized by fish with small size at age in the younger ages but whose growth rate relative to southern capelin accelerates with age to produce as large a maximum size; 3K capelin,

intermediate in geographical location have also an intermediate growth rate. This cline in growth from south to north is also reflected in maturation rate (Winters 1974a), Labrador capelin tending to mature about a year later than Grand Bank capelin. Such spatial variations are attributed by Winters (1974a) to temperature effects, both directly, and indirectly through attrition in the duration of the growing season from south to north.

Mortality and yield

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

Trophic relationships of capelin

Capelin are undoubtedly the most important fish fodder resource in the Canadian Atlantic area, being preyed on by a wide variety of commercial fish species, mammals and seabirds (Templeman 1967; Campbell and Winters 1973). Herein lies the main crux of the capelin problem; how much and in what way can the capelin resource be reduced by a fishery without undue detriment to its main predators, particularly cod which because of their abundances, size and feeding habits are the main predator of capelin. From the Murmansk coast westwards to Iceland, Greenland, Labrador, Newfoundland and the Gulf of St. Lawrence cod migrate inshore in large numbers in pursuit of capelin during their spawning migration to coastal waters (Ulltang 1974; Jangaard 1974). In the Newfoundland area capelin comprise over 90% of the diet of cod during June and July (Campbell and Winters 1973) and nearly 32% on an annual basis. Capelin are also the main prey species of Atlantic salmon in the Northwest Atlantic (Lear 1972) and in Newfoundland coastal waters accounts for 45-100% of the food of salmon depending

on size. Greenland halibut in the length range 20-80 cm feed almost exclusively on capelin (Lear 1969); American plaice in the size range 20-39 cm in ICNAF Subdivision 3L depend on capelin for 30-38% of their food supply (Pitt 1973). Haddock, yellowtail flounder, winter flounder, skates, sea ravens and a variety of other incidental species of groundfish consume large quantities of capelin eggs and capelin during the spawning season (Pitt 1958a; Templeman 1968). Large pelagic fish such as bluefin tuna also feed extensively on capelin in the Newfoundland area and small pelagics such as herring and mackerel often feed on capelin larvae and juveniles (Moore, personal communication).

Marine mammals also feed heavily on capelin. In the Northeast Newfoundland Shelf in 1947-51 capelin were the dominant prey species in 90% of the fin whale (Balaenoptera physalus) stomachs examined and in 1967-71 were almost the exclusive food of fin whales (Mitchell, in press). Sargeant (1963) reported that capelin were found in 85% of the stomachs of minke whales (Balaenoptera acutorostrata) caught commercially in Newfoundland. Other less abundant whales such as the sei whale (Balaenoptera borealis) also eat substantial quantities of capelin.

Harp seals (Pagophilus groenlandicus) breed in large numbers along the Newfoundland Shelf and in the Gulf of St. Lawrence and Sargeant (1973) estimated that at least 25% of their diet consisted of capelin. Other species of seals (hood, grey and harbour) although less abundant also consume significant quantities of capelin.

Capelin form the main food supply of many seabirds in Subarea 2-3. Alcids, particularly thick-billed murres which over-winter along eastern Newfoundland depend on capelin for 90% of their diet; approximately 7,000,000 Greater Shearwaters feed in the Newfoundland area during the summer period and depend heavily on capelin for their food (Brown, personal communication); a wide variety of other less numerous seabirds such as puffins, gannets and kittiwakes also feed heavily on capelin.

Capelin as a limiting factor in the production of its major predators

All of the major predators of capelin (cod, harp seals, and fin whales) have been characterized by severe attritions in biomass levels in the past several decades as a result of intensive fisheries for those species. For example, in the early 1950's the harp seal population in the Northwest

Atlantic was near its asymptotic level, being estimated by H. D. Fisher in 1950-51 at 3×10^6 animals; by the late 1960's intensive harvesting had reduced the population to 1.3×10^6 animals (Sergeant 1973). Similarly, the extensive international fisheries for cod which developed in Subareas 2-3 in the late 1950's reduced the cod population to about half its former level (see later sections). If food were a limiting factor to the production and abundance of these predators such major population changes would be expected to be reflected in such population parameters as growth rate, maturation rate, fecundity, recruitment and natural mortality. Changes in these parameters are investigated below for the three major capelin predators.

A. Cod. A large proportion of the annual growth of cod in the Newfoundland area is deposited during the period June-August (Templeman 1965) at which time capelin comprise almost the exclusive component of their diet. Consequently, the availability of capelin per unit biomass of cod should be a major factor influencing changes in cod growth. Wells and Pinhorn (MS 1970) compared Bertalanffy growth parameters of cod stocks in Subareas 2-3 from the early to the late 1960's and demonstrated a general growth increase for all stocks which they attributed to the reduction in the numbers of older fish by the commercial fishery. Data on cod growth in Subdivision 3KL prior to the period of heavy exploitation are available from Hodder (1964) for the period 1947-57. Population numbers by age of 3L cod back to 1955 and 2J3KL cod back to 1961 are available from Pinhorn and Wells (1972). From average ratios (by age) of 3L to 2J3KL cod in 1961-62, the total population size of 2J3KL cod back to 1955 has been calculated and averaged for the period 1955-57. A comparison of population numbers and weight at age of 2J3KL cod (3KL during 1947-57, combined in proportion to relative population size, with 2J for 1960-62) before (1947-62) and after (1964-68) heavy exploitation is shown in Table 3. Substantial compensatory growth increases have occurred in 2J-3KL cod since the 1950's, the differences tending to increase with age to the extent that a 14-year-old cod in 1964-68 was nearly 80% greater in weight than a cod of the same age in 1947-62. The increasing growth differences with age is apparently a density-dependent response to the greater reduction in the numbers of older fish compared with younger age-groups. A plot of the changes in age-specific weights in relation to changes in population number (Fig. 3) produces a linear relationship with a highly significant correlation ($r = .80$).

Table 3. Comparison of age-specific weights and population numbers (millions of fish) of 2J3KL cod before (1947-62) and after (1964-68) heavy exploitation.

Age	W_t (Kg)		ΔW_t (%) $\left(\frac{b-a}{a}\right)$	N_t		$\frac{\Delta N_t}{N_t}$ $\left(\frac{\sum_{t=14+} N(c) - \sum_{t=14+} N(d)}{\sum_{t=14+} N(d)}\right)$
	1947-62 (a)	1964-68 (b)		1955-57 (c)	1964-68 (d)	
4	.50	.57	14.0	452	678	0.35
5	.75	.94	25.3	445	508	0.71
6	1.12	1.28	14.3	351	311	1.26
7	1.40	1.75	25.0	299	200	2.04
8	1.71	2.27	32.7	386	113	3.20
9	1.99	2.68	34.7	250	60	3.81
10	2.14	3.13	46.3	198	32	4.26
11	2.27	3.57	57.3	97	18	3.70
12	2.39	4.06	69.9	50	11	3.36
13	2.54	4.50	77.2	40	8	4.28
14	2.69	4.81	78.8	22	5	3.94
14+	3.06	5.25	71.6	45	12	3.75
$\overline{\Delta W_t}$ (unweighted)			54.3	$\overline{\Delta N_t}$		0.35
$\overline{\Delta W_t}$ (weighted)			26.5	$\overline{\Delta B_t}$		0.55

The mean weight of 2J3KL cod, weighted according to the population age structure in 1964-68 increased by 26.5% from 1947-62 to 1964-68. Over the same period the population numbers declined 35% whereas the biomass was 55% greater in 1955-57 than in 1964-66. Assuming that cod were able to take full advantage of the increased availability of food per unit biomass in the latter period, the decrease in biomass level implies an increase (perhaps commensurate) in ration size per unit biomass. According to Paloheimo and Dickie (1966) gross growth efficiency (log K) decreases with increase in ration size according to the formula $\log K = \log (DW/RDt) = a-bR$, which upon transformation becomes $\frac{DW}{Dt} = Re^{a-bR}$. This produces an asymptotic relationship between growth

and ration size which implies that increasing the food supply beyond a certain level will not lead to further increases in growth rate due to changes in energy conversion efficiency (log K). Thus a decrease in log K in response to the increased ration size available per unit biomass of cod as a result of a biomass reduction is probably-responsible for the observed growth increase (26.5%) being substantially less than would be expected from the reduction in stock size.

Insofar as maturation rate and fecundity of cod are concerned specific data are not available although, as would be expected, changes in the age at maturity have apparently occurred (Wells, personal communication). Recruitment variations have also been investigated for density-dependent effects (see following table).

Recruitment estimates (at age 4) of 2J-3KL cod for the year-classes 1955-67. (Data from Pinhorn and Wells, 1972, 1974, and personal communication).

	Year-classes												
	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967
Recruitment (x 10 ⁻⁶)	840	584	907	485	612	506	629	762	908	581	542	605	510
	$\bar{R} = 656$						$\bar{R} = 648$						

Recruitment of 2J-3KL cod has remained constant, at least for the year-classes between 1955 and 1967. This suggests that increases in maturation rate and fecundity have been substantial enough to maintain population fecundity at a high level, although it is possible that the time lag has not been sufficiently long to allow recruitment changes to show up.

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

B. Seals. Available evidence on the feeding of harp seals has been summarized by Sergeant (1973). After the intensive harvesting of harp seals through the 1950's and early 1960's maturation rates increased (Sergeant 1966)

implying an increase in growth rates (Laws 1959). Sergeant also noted that moulting adults were in much better condition and fat thickness was greater in the late 1960's than a decade or so earlier when population levels were high.

Data are not available on trends in recruitment and natural mortality of harp seals although the better condition of the adults together with the increased maturation rate has undoubtedly increased the maternal frequency, survival rate of the young and net reproductive rate of the population as a whole.

C. Whales. Fin whales, balaenoptera physilus, together with harp seals are the dominant sea mammal predators on capelin (Sergeant, personal communication) in the Newfoundland Shelf area. About 5000 fin whales have been estimated to summer off the Newfoundland coast from May to November (Allen 1971). No data are available on trends in population parameters of fin whales although Sergeant (personal communication) noted wide annual variations in oil yields in the period 1947-51, whereas Mitchell (in press) found very little variation in availability of capelin in fin whale stomachs in 1967-71. Since fin whales were heavily exploited in 1947-51 the temporal contrast can only be explained by the lesser availability of capelin during 1947-51 due to the greater predator of near-asymptotic populations of cod and harp seals. It therefore appears that similar increases in growth, maturation and net reproduction have occurred in fin whales as in harp seals.

Identification of capelin stocks

On the basis of seasonal distributions and probable migration patterns Campbell and Winters (1973) suggested that the capelin resource in Subareas 2 and 3 could be partitioned into the following stocks; (1) Labrador-Northeast Newfoundland stock; evidence for this stock is based mainly on Soviet surveys from September-December 1972 (Kavolyov and Kudrin 1973) which indicated that capelin in the Hamilton Bank area migrated southwards during the autumn to over-winter in the Notre Dame Bay area between $50^{\circ}00'-51^{\circ}00'N$ and $52^{\circ}30'-54^{\circ}00'W$ in 3K; these capelin presumably spawn on inshore beaches in 3K during the following summer; (2) Northern Grand Bank-Avalon stock based mainly on inferences from tagged cod which migrated from the northwestern part of Grand Bank in early June to the Avalon Peninsula (Fig. 1) during the capelin spawning season in that area; (3) Southeast Shoal stock; this was assumed to be a separate spawning stock from other areas due to the concurrence of spawning times of

inshore and Southeast Shoal capelin; (4) St. Pierre-Green Bank stock based mainly on Norwegian surveys which indicated that concentrations of mature capelin in the Green Bank area (30) in May were not recorded there in June and presumably had moved westwards to spawn either on St. Pierre Bank or inshore in 3Ps.

Winters (1974b) reviewed stock discrimination data at the 1974 Mid-term Meeting and summarized new information which indicated that inshore capelin from 3K and Subarea 2 comprise different stocks with different growth characteristics but which possibly intermingle offshore in the summer-fall period in 2J. In addition Winters (1974b) hypothesized, on the basis of Soviet (Kovalyov and Kudrin 1973), Canadian (Campbell and Winters 1973) and Norwegian (Dragesund and Monstad 1973) surveys and comparison of growth curves (Fig. 2) that northern Grand Bank was a feeding and over-wintering area for both Southeast Shoal and inshore (3L) spawners as well as a nursery area for immature capelin. STACRES subsequently recommended that a minimum stock division, incorporating probable stock mixtures, would include 2-3K as one stock complex and 3LNOPs as another complex with the larger portion of the 1974 TAC being allocated to the southern stock on the basis of the desired expansion of the capelin fishery in that area by new entrants.

During April-June 1974 a new fishery for pre-spawning capelin was initiated by the Soviet fleet in the Avalon Channel area in 3L (Fig. 1), starting in the north in April and gradually moved southwards, terminating in the Nickerson Bank-Green Bank area (Fig. 1) in early June. At the 1974 Annual Meeting the Assessments Subcommittee recognized the existence of this new fishery but did not recommend a further partition of the TAC due to a lack of biological data on the stock relationships of these capelin. The St. John's Biological Station through its research vessel surveys and commercial sampling system has collected age and growth data on the Avalon Channel capelin as well as adjacent areas for several years and such data are evaluated below in relation to the stock components of 3LNOPs capelin.

Age compositions of mature capelin from inshore and offshore areas of 3LNOPs in 1974 are compared in Fig. 4. Capelin from northwestern Grand Bank (3L), Nickerson Bank (3L) and the Southeast Shoal had almost identical age compositions in 1974; those from Fortune Bay (3Ps) were distinctly different in year-class composition from other areas; beach-spawning capelin from Bonavista Bay and the Avalon Peninsula were characterized by age composition somewhat

similar to offshore samples in 3LN, but contained either a higher proportion of younger fish (Avalon) or older fish (Bonavista Bay). Comparison of mean size-at-age (Table 4) indicates that differences in growth are neither large enough nor consistent enough to provide significant stock discrimination evidence. Similar results were obtained by Winters (1974a) from back-calculated data. Fig. 5 illustrates age composition histograms of mature capelin for selected areas in 3LNO for the years 1967-68, 1972-73. The 1967 inshore samples from the Avalon Peninsula and Trinity Bay were more closely related to each other than Southeast Shoal capelin which was dominated by much younger fish. In 1968, however, inshore samples from Trinity Bay and the Avalon Peninsula were very similar to the offshore samples from the Southeast Shoal and northwestern Grand Bank. Similarly in 1972 and 1973 inshore spawners from the Avalon area were identical in age composition to offshore samples from the Southeast Shoal and northwestern Grand Bank.

Table 4. Mean lengths-at-age of mature capelin sampled in various areas in 3LNOPs during 1974.

Area	Mean size at age (mm)					
	Males			Females		
	3	4	5	3	4	5
N.W. Grand Bank	178	188	189	156	173	177
Nickerson Bank	179	189	190	160	172	178
Southeast Shoal	182	190	193	161	169	176
Fortune Bay	183	189	195	168	175	176
Avalon Peninsula	180	188	191	152	170	172
Bonavista Bay	184	190	192	165	175	179

In summary, the above data suggest the following conclusions:
 1) Fortune Bay (3Ps) capelin are probably a separate stock from capelin in 3LNO; 2) the similarity between northwestern Grand Bank and Southeast Shoal in all years indicate that these are part of the same population; 3) the inconsistency in the age compositions of inshore capelin in 3L compared to offshore capelin from Grand Bank is interpreted to represent separate stocks which either do not mix or intermingle in varying proportions from year to

year perhaps in response fluctuations in year-class strength, large year-classes tending to intermingle more than weak year-classes. There is certainly an abundance of capelin in coastal areas during the winter-spring period at the same time large concentrations of capelin have also been reported on the northern portion of Grand Bank - this is indicated by (1) occurrence of capelin in stomachs of cod, turbot, murre, salmon, etc., in inshore areas; (2) mass mortalities of inshore capelin during the winter period (Templeman 1948); (3) Canadian research and exploratory surveys (Winters 1970); (4) incidental catches of capelin by commercial fishing vessels in coastal bays. Whether such coastal capelin form separate stocks from that offshore or merely represent extensions of the over-wintering area is uncertain but evidence suggests that some mixing does occur. The migrations of cod from the northwestern portion of Grand Bank in June are well documented (Templeman and Fleming 1962), and it is likely they are in pursuit of capelin; movements of the Soviet capelin fleet in 1974 from the northwestern portion of Grand Bank in April to within 15 miles of the Avalon Peninsula in late May also suggest an inshore migration as well as a southern migration. It therefore seems more plausible to suggest that some mixture of inshore and offshore capelin occurs in 3L but that the proportion may vary from year to year.

Estimation of surplus yield of capelin

The major predators of capelin in the Northwest Atlantic area (cod, seals and whales) have all suffered major reductions in population sizes over the past several decades. If data were available on the magnitude of the decline, and consumption rates of capelin before and after exploitation a simple deterministic model can be constructed which can provide some idea as to the amount of excess production released by the decline in those predators and available to a fishery. Some data relevant to such a simulation model are available, particularly for cod; where data aren't available I have made reasonable assumptions based on the best advice possible. The model is presented below, the basic implied assumption being that the production of capelin is independent of predator dynamics.

I. Calculation of surplus production released by cod decline.

A. Attrition in cod biomass

1. Current and MSY stock-size ('000 m. tons).

Stock	MSY	F_{max}	MSY stock size ¹	Current stock size ²
2GH	30	0.70	85	85
2J3KL	550	0.35	2050	2200
3NO	100	0.20	600	575
3Ps	60	0.30	250	300
Total	740		2985	3160

1 - Calculated from Baranov catch equation.

2 - Pinhorn and Wells (1974).

2. Estimate of initial (unexploited) stock size (B_0).

a) 2J3KL Cod stock. This is the largest cod stock in the area; it has the longest time series of data and is taken as being representative of other cod stocks in Subareas 2-3.

Theoretical Considerations: 1) Shaefer (1954) (logistic) model predicts B_0 to be twice the MSY level, i.e. $2.05 \times 2 = 4.1$ mill. m. tons.
 2) Yield per recruit model with growth, natural mortality and recruit parameters applicable to 2J3KL cod predicts MSY level to occur at approximately 40% of B_0 (Gulland 1971), i.e. $B_0 = MSY \times 2.5 = 2.05 \times 2.5 = 5.1$ mill. m. tons.

Calculated prior to heavy exploitation: From the ratio (by age) of 3L (Wells 1972) to 2J3KL (Pinhorn and Wells 1972) cod in 1961-62, average stock size of 2J3KL cod during 1955-57 was calculated from Table 3 to be 3.6 mill. m. tons. Since this stock sustained an annual catch of over 200,000 m. tons during this period (Templeman 1966), the above estimate is a minimum estimate of B_0 .

$$\begin{aligned} \therefore \text{Mean estimate of } B_0' \text{ (2J3KL)} &= \frac{4.1 + 5.1 + 3.6}{3} \\ &= 4.27 \text{ mill. m. tons} \\ &= 2.08 \times \text{MSY level.} \end{aligned}$$

b) Extrapolation of ratio of B_0 to MSY

$$\begin{aligned} \text{Stock size for all cod stocks} &= 2.985 \times 2.08 \\ &= 6.21 \text{ mill. m. tons.} \end{aligned}$$

3. Calculation of annual consumption rate of capelin per unit weight of cod (R):

a) R_0 (Theoretical)

In equilibrium state $P_0/B_0 = z = 0.2$

$$\begin{aligned}\therefore P_0 &= B_0 \times 0.2 \\ &= 6.20 \times 0.2 \\ &= 1.24 \text{ mill. m. tons.}\end{aligned}$$

Also $P_0 = KI_0$ where K = growth efficiency

I_0 = food intake.

An average estimate of $K = 0.1$ (Slobodkin 1962)

$$\begin{aligned}\therefore \text{total food intake of cod at } B_0 &= P_0/K \\ &= \frac{1.24}{.1} \\ &= 12.4 \text{ mill. m. tons.}\end{aligned}$$

During the period 1947-51 capelin represented 32% of the food intake of cod (Campbell and Winters 1973).

$$\begin{aligned}\text{Thus, the annual consumption of capelin by cod at } B_0 \text{ (} C_0 \text{)} &= 12.4 \times 0.32 \\ &= 3.97 \text{ mill. m. tons}\end{aligned}$$

$$\begin{aligned}\text{Whence } R_0 &= C_0/B_0 \\ &= \frac{3.97}{6.21} \\ &= 0.64 \text{ units of capelin per unit cod weight.}\end{aligned}$$

b) R_c

1. For the 1965-70 pentade Campbell and Winters (1973) estimated R in the range of 0.5-1.0; best empirical estimate is $0.7 \geq R_c \leq 1.0$.

2. From 1955-57 to 1964-68 the reduction in 2J3KL cod biomass increased the nominal availability of food per unit biomass of cod 55% which produced a density-dependent growth increase of only 26.5%. Because of the relationship between ration size and growth efficiency it is probable that the food consumption of cod increased more than the rate at which growth increased; it is unlikely, however, that cod were able to take full advantage of the increased availability of capelin due to the fact that not all cod migrate to shore in pursuit of capelin and this is particularly so with regards to the younger cod which characterize the present cod age structure in the northern areas. Thus the halving of the virgin cod biomass through fishing is unlikely to have resulted in a doubling of R_0 . Consequently, as a liberal estimate of R_c the upper limit of the empirical range has been selected, i.e. $R_c = 1.0$. This represents a 56% density-dependent increase in R_0 .

4. Thus, the surplus production of capelin released by the decline in cod stocks = $C_D - C_C$
= $3.97 - (1.0 \times 3.0)$
= .97 mill. m. tons.

B. Attrition in seal population

The current population of harp seals in the Northwest Atlantic is estimated to be 1.3×10^6 animals. This compares with 3.0×10^6 animals prior to the recent period of heavy exploitation. The asymptotic level in numbers is in all likelihood greater than 3.0×10^6 but taking into account the density-dependent increase in growth it is a reasonable statement that the present biomass of seals (B_C) is about $\frac{1}{2}$ the initial level (B_0).

Sergeant (1973) estimates that 400,000 m. tons of capelin are consumed by seals at present, of which (from over-wintering proportions) about 300,000 m. tons (= C_C) are taken off eastern Newfoundland and Labrador. Assuming that harp seals have demonstrated equivalent increases in growth (26%) and consumption rate per unit biomass (56%) as cod, the annual consumption of capelin by seals in the virgin state (C_0) is therefore calculated as follows:

$$\begin{aligned} C_0 &= C_C \cdot (B_0/B_C - 0.56) \\ &= 300,000 \cdot (2.0 - 0.56) \\ &= \hat{=} 430,000 \text{ m. tons.} \end{aligned}$$

Thus, the surplus production of capelin released by the decline in the harp seal population = $430,000 - 300,000 = 130,000$ m. tons.

C. Whales

a) Fin whales. The current population of fin whales in the Newfoundland Shelf area is approximately 2500 animals (Sergeant, personal communication), which is about half of the former level (Mitchell 1972). From data on feeding rates of fin whales (Sergeant 1971) it is estimated that each whale consumes about 100 m. tons of capelin during the summer feeding season in the Newfoundland area. Thus the current consumption of capelin by the fin whale population is 250,000 m. tons. Assuming the same changes in R as occurred in cod, the initial consumption of capelin (C_0) by fin whales = $C_C \cdot (B_0/B_C - 0.56)$
= $250,000 \cdot (2.0 - 0.56)$
= 360,000 m. tons.

Whence the surplus production of capelin released by fin whales

= 360,000-250,000

= 110,000 m. tons.

b) Other whales. Minke whales are abundant in the Newfoundland area and depend heavily on capelin for their food supply (Sergeant 1963). Sergeant (personal communication) estimates their daily consumption rate of capelin to be 0.13 that of fin whales which, extrapolated to a seasonal basis, indicates a current consumption of about 35,000 m. tons of capelin. Assuming the same change in population numbers and consumption rates as with fin whales this suggests that about 15,000 m. tons of capelin have been released by the decline in the Minke whale population.

c. Thus the total surplus production of capelin released by the decline in whale numbers is in the order of 125,000 m. tons.

D. In summary, the total excess production of capelin released by the decline in the abundance of its major predators = $0.97 + 0.13 + 0.13$

= 1.25 mill. m. tons.

Discussions and Conclusions

The above estimate of excess yield of capelin derived from predator interactions should only be interpreted to indicate in a crude manner the order of magnitude of potential capelin yield, under the assumptions used in the model. The most critical of these assumptions relate to steady-state conditions insofar as capelin production is concerned, and to the constancy of the relative diet composition of the major predators. Insufficient data prevent a detailed evaluation of the adherence of these assumptions but the general deterioration of temperature conditions over the past several decades (Rodewald 1972) suggest that capelin production is lower now than formerly; this is reflected in the reduced growth rate and older age at maturity of Grand Bank capelin in recent years (Winters and Campbell 1974). It is unlikely that capelin have increased in relative importance at least in the diet of cod since historical feeding studies show that capelin form a significant proportion of cod food only during the spawning season of capelin in June-July at which time they constitute almost the exclusive diet of cod. It is also unlikely that the present cod populations, characterized as they are by young fish, have been able to take full advantage of the increased availability of capelin per unit cod biomass: this is suggested by the much greater growth increases (up to 80%) observed in the older cod which

migrate to shore in greater proportions than younger fish at least in the northern areas (Pinhorn, personal communication).

Density-dependent changes in growth, and maturity have been demonstrated for the major capelin predators, particularly cod. The effects of over-exploitation of capelin (either a direct reduction in the food supply of the major predators, or indirectly through recruitment failure of capelin) can therefore be expected to reverse at least some of these changes. For cod, a decrease in growth rate will almost certainly occur with associated concomitant changes in maturation rate and fecundity. If fishing mortality on cod continues to be regulated at the present level, this implies a significant drop in population fecundity which may or may not result in recruitment loss, depending on the stock-recruit relationship of cod. Thus, a minimum effect on cod would be a drop in yield per recruit, perhaps accompanied by an increase in natural mortality and a decrease in recruitment. For sea mammals similar changes in growth and maturity may be expected which would in all probability cause a decrease in net reproductive rate and thus population levels. If the capelin ecosystem in Subareas 2-3 is already being fully exploited, the effects of a human fishery on the major predators should appear fairly soon. For example, the Humboldt current anchoveta population has fluctuated rather dramatically in response to environmental variations which were soon reflected in parallel changes in the predator bird populations (Shaefer 1970). Thus the development of an intensive and highly-competitive human fishery for anchovy in the late 1950's resulted almost immediately in a dramatic decline in the bird population which has remained at low levels since then. A second example relates to the Bering Sea fur seal population which depend heavily on the Alaska pollock Theragra chalcogramma as its major prey resource. In recent years an intensive fishery for pollock has removed most of its capital stock with the result that substantial reductions in growth, net reproductive rate and recruitment have shown up in the fur seal population (Joseph et al. 1974; Sergeant, personal communication).

Although the potential yield of a capelin fishery may be large, the heavy spawning mortality of capelin implies that both stock size and potential catch will fluctuate directly in response to recruitment variations, which may be substantial. For Barents Sea capelin during the period 1951-61 recruitment (estimated from catch-per-unit-effort data) fluctuated by a factor of 17 times, the lowest estimate being only 20% of the average for the period (Gjøsaeter 1972).

Over the same interval the parent stock fluctuated by a factor of 11 times, the lowest abundance estimate being 20% of the average. Information on fluctuations in biomass and recruitment of Northwest Atlantic capelin is scanty and no direct information is available as to the specific levels of spawning stock and recruitment which will support the 1975 fishery. In the absence of such information, the 1975 TAC for capelin in Subareas 2-3 should not exceed the lower limit of fluctuations in spawning stock size, particularly in view of the possibility of successively poor year-classes resulting from severe hydrographic conditions existing since 1971. Taking 1.25 mill. m. tons as one estimate of sustainable yield of capelin and 20% as the lower range of spawning stock fluctuation implies a TAC of 250,000 m. tons in 1975.

Further partitioning of the capelin TAC would also be desirable in 1975. Age composition data indicates that 3Ps capelin belong to a different stock than 3LNO capelin and consequently should be allocated a separate TAC. The capelin stock which supported the new fishery in 3L during 1974 should also be allocated a separate TAC, particularly if, as the author has hypothesized, 3L is a mixing area for inshore and offshore-spawning capelin. Since the 1974 fishery in 3L was based on pre-spawning capelin, the TAC for that component should be relatively small in order to reduce the possible effect of fishery removals on inshore cod migrations and also because of the general desirability of restricting capelin fisheries to the spawning season: such fisheries not only take a significant proportion of spent fish but also ensure that juvenile capelin are not being exploited and that cod migrations suffer minimal effects. Interpretation of the stock relationships of Subarea 2 and 3K capelin is not clear but to prevent excessive exploitation of any one stock by "floating" effort it would be a desirable management action to partition the northern capelin TAC into at least two components, Subarea 2 and 3K.

The importance of annual resource inventory and recruitment surveys of capelin cannot be over-emphasized, if future TAC's are to be directly related to relative changes in capelin abundance. Countries participating in the capelin fishery in Subareas 2-3 should therefore make every effort to institute such surveys on a regular basis, beginning in 1975.

Acknowledgments

The author wishes to express his gratitude to Dr D. E. Sergeant and Dr P. Brodie for their advice on sea mammal ecology and dynamics in the Northwest Atlantic. Particular acknowledgments are due Messrs A. T. Pinhorn and R. Wells of the St. John's Biological Station, who gave freely of their time, advice and cod data in the development of the model of surplus production.

References

- Campbell, J. S. and G. H. Winters. 1973. Some biological characteristics of capelin, Mallotus villosus in the Newfoundland area. Intern. Comm. Northw. Atlant. Fish. Redbook, Part III, 1973: 137-144.
- Dragesund, O. and T. Monstad. 1973. Observations on capelin (Mallotus villosus) in Newfoundland waters. Intern. Comm. Northw. Atlant. Fish. Redbook, Part III, 1973: 127-136.
- Gjøsaeter, J. 1972. Recruitment of the Barents Sea capelin 1951-61. ICES C.M. 1972/H: 24.
- Gulland, J. A. 1971. The fish resources of the ocean. Fishing News (Books) Ltd., Surrey, England, 255 p.
- Hodder, V. M. 1964. Assessments of the effects of fishing and of increases in the mesh size of trawls on the major commercial fisheries of the Newfoundland area. Fish. Res. Board Can. MS. Rept. Biol. No. 801, 116 p.
- Jangaard, P. 1974. The capelin (Mallotus villosus). Biology, distribution, exploitation, utilization and composition. Fish. Res. Board Can. Bull. No. 186, 70 p.
- Joseph, L., James P. and W. L. Klave. 1974. The living pelagic resources of the Americas. Ocean Dev. and Inter. Law J. Vol. 2 (1): 37-64.
- Kovalyov, S. M. and B. D. Kudrin. 1973. Soviet investigations on capelin on the Grand Bank of Newfoundland in 1972. Intern. Comm. Northw. Atlant. Fish. Res. Doc. 73/26, Ser. No. 2959: 4 p.
- Laws, R. M. 1959. Accelerated growth in seals, with special reference to Phocidae. Norsk Hvalfangst-Tid. 1959 (9): 425-452.

- Lear, W. H. 1969. The biology and fishery of the Greenland halibut (Reinhardtius hippoglossoides) in the Newfoundland area. M. Sc. Thesis, Memorial University of Newfoundland, 1969.
1972. Food and feeding of Atlantic salmon in coastal areas and over oceanic depths. Intern. Comm. Northw. Atlant. Fish. Res. Bull. No. 9: 27-39.
- Mitchell, E. 1972. Assessment of Northwest Atlantic fin whale stocks. Annex L, Intern. Comm. Whaling. 22nd Rept., London, p. 111-118.
- Paloheimo, J. E. and L. M. Dickie. 1966. Food and Growth of Fishes. III. Relations among food, body size and growth efficiency. J. Fish. Res. Board Can. 23 (8): 1209-1248.
- Pinhorn, A. T. 1972. Estimates of natural mortality for ICNAF Division 2J cod. Intern. Comm. Northw. Atlant. Fish. Res. Doc. 72/2, Ser. No. 2681, 7 p.
- Pinhorn, A. T. and R. Wells. 1972. Combined vertical population assessment for ICNAF Divisions 2J, 3K, and 3L cod. ICNAF Res. Doc. 72/109: 6 p.
1974. Calculation of total allowable catches (TAC's) for 1975 for the cod stocks in Subareas 2 and 3. Intern. Comm. Northw. Atlant. Fish. Res. Doc. 74/89, Ser. No. 3325, 16 p.
- Pitt, T. K. 1958. Age and growth of the capelin, Mallotus villosus (Miller) in the offshore Newfoundland area. J. Fish. Res. Board Can. 15: 295-311.
1973. Food of American plaice (Hippoglossoides platessoides) from the Grand Bank, Newfoundland. J. Fish. Res. Board Can. 30: 1261-1273.
- Rodewald, M. 1972. Temperature conditions in the North and Northwest Atlantic during the decade 1961-70. Intern. Comm. Northw. Atlant. Fish. Spec. Publ. No. 8: 9-33.
- Sergeant, D. E. 1963. Minke whales, Balaenoptera acutorostrata, Lapepe of the western North Atlantic. J. Fish. Res. Board Can. 20: 1489-1504.
1966. Reproductive rates of harp seals, Pagophilus groenlandicus (Erxleben). J. Fish. Res. Board Can. 23: 757-766.
- 1973a. Feeding, growth and productivity of Northwest Atlantic harp seals. J. Fish. Res. Board Can. 30: 17-29.
- 1973b. Environment and reproduction in seals. J. Reprod. Fert. Suppl. 19: 555-561.

- Shaefer, M. B. 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Inter-Amer. Trop. Tuna Comm. Bull. 1 (2): 27-56.
1970. Men, birds and anchovies in the Peru Current-Dynamic Interactions. Trans. Amer. Fish. Soc. Vol. 99 (3): 461-470.
- Slobodkin, L. B. 1962. Energy in Animal Ecology. Adv. Ecol. Res. 1: 69-101.
- Templeman, W. T. 1948. The life history of the capelin (Mallotus villosus) in Newfoundland waters. Bull. Nfld. Gov't. Lab. No. 17: 1-151.
1965. Some instances of cod and haddock behaviour and concentrations in the Newfoundland and Labrador areas in relation to food. Intern. Comm. Northw. Atlant. Fish. Spec. Publ. No. 6: 449-461.
1966. Marine resources of Newfoundland. Bull. Fish. Res. Board Can. 154: 170 p.
1967. Capelin distribution, spawning, migrations, concentrations and abundance in the Canadian area of the Northwest Atlantic. Conference on Comm. Poss. of capelin. Can., Dep. Fish. Ottawa, Feb. 1, 1967, 22 p.
1968. Review of some aspects of capelin biology in the Canadian area of the Northwest Atlantic. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer. 158: 41-53.
- Templeman, W. T. and A. M. Fleming. 1962. Cod tagging in the Newfoundland area during 1947 and 1948. J. Fish. Res. Board Can. Vol. 19 (3): 445-487.
- Ulltang, O. 1974. On the management of a capelin fishery. Intern. Comm. Northw. Atlant. Fish. Res. Doc. 74/90, 7 p.
- Wells, R. 1972. Virtual population assessments of cod in ICNAF Divisions 3K and 3L. Intern. Comm. Northw. Atlant. Fish. Res. Doc. 72/16, Ser. No. 2700, 10 p.
- Wells, R. and A. T. Pinhorn. 1970. Growth and mortality changes in cod from ICNAF Subareas 2 and 3. Intern. Comm. Northw. Atlant. Fish. Res. Doc. 70/88, Ser. No. 4239, 5 p.
- Winters, G. H. 1970. Biological changes in coastal capelin from the overwintering to the spawning conditions. J. Fish. Res. Board Can. Vol. 27 (12): 2215-2224.
- 1974a. Back-calculation of the growth of capelin (Mallotus villosus) in the Newfoundland area. Intern. Comm. Northw. Atlant. Fish. Res. Doc. 74/7, Ser. No. 3150, 16 p.

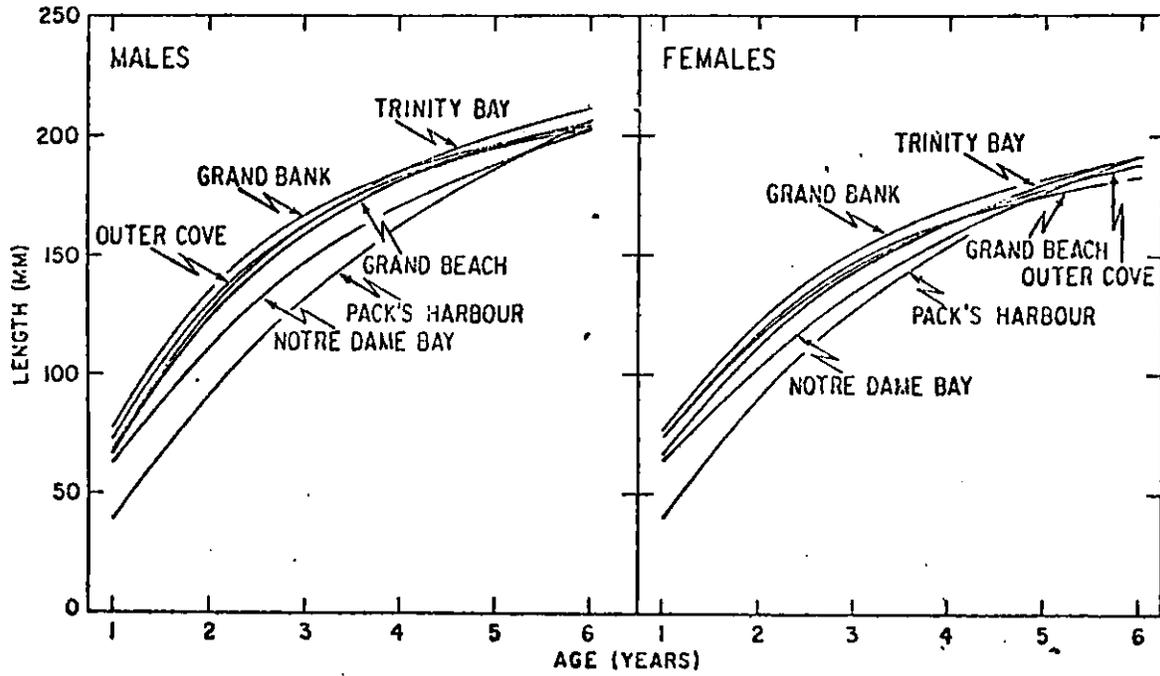


Fig. 2. Comparison of von Bertalanffy growth curves of capelin from various localities in the Newfoundland-Labrador area (from Winters 1974a).

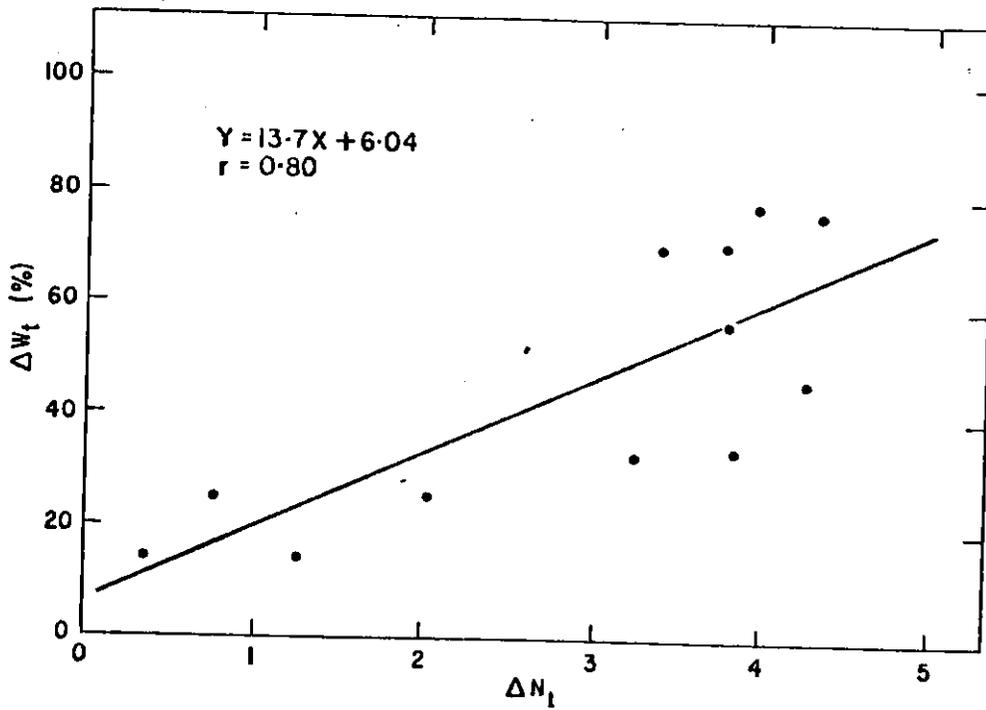


Fig. 3. Plot of changes in age-specific weights of 2J3KL cod from 1947-62 to 1964-68 in relation to changes in population numbers over the same period (see Table 3).

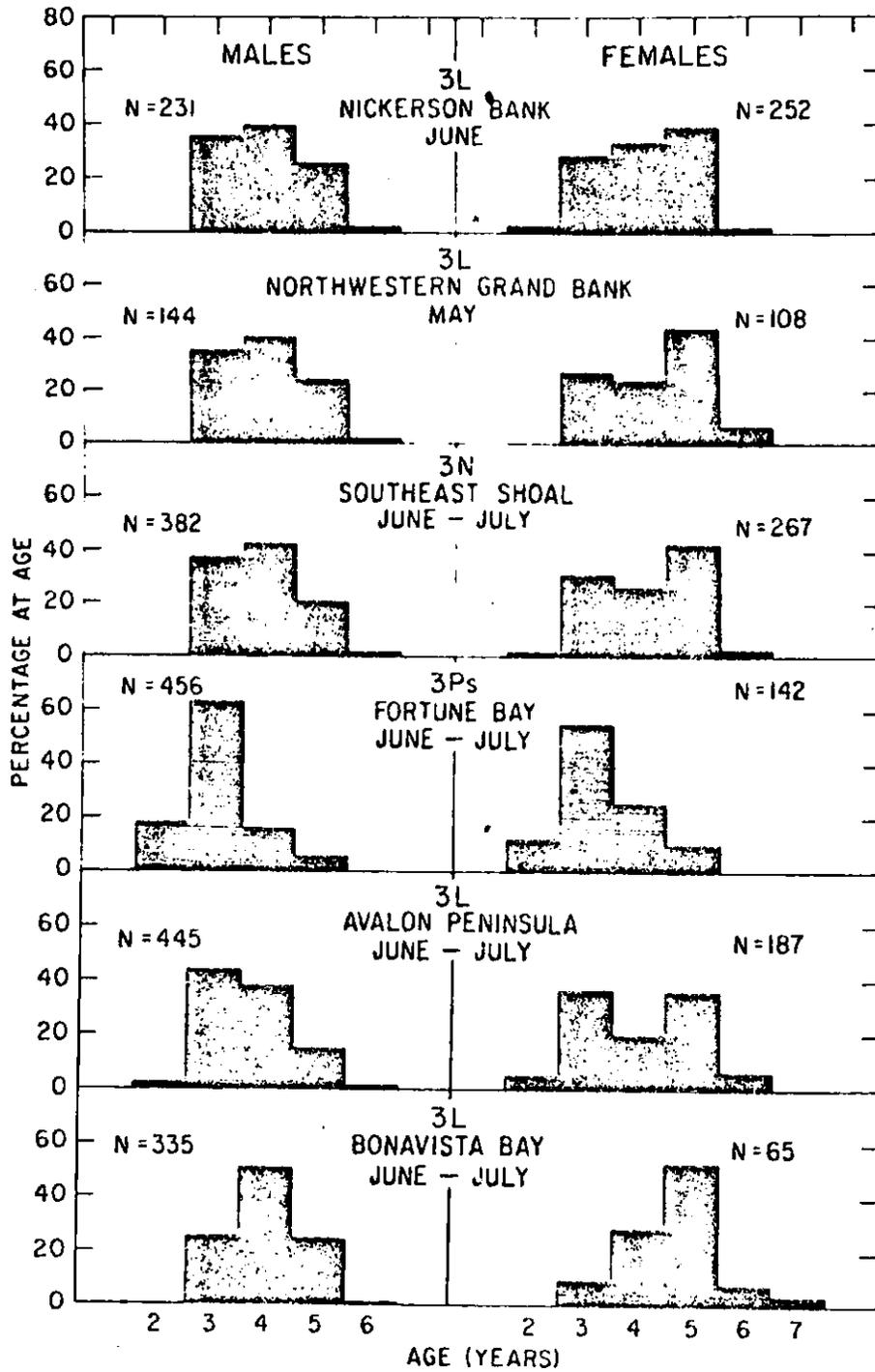


Fig. 4. Age compositions of mature capelin from inshore and offshore areas in Divisions 3LNOPs in 1974.

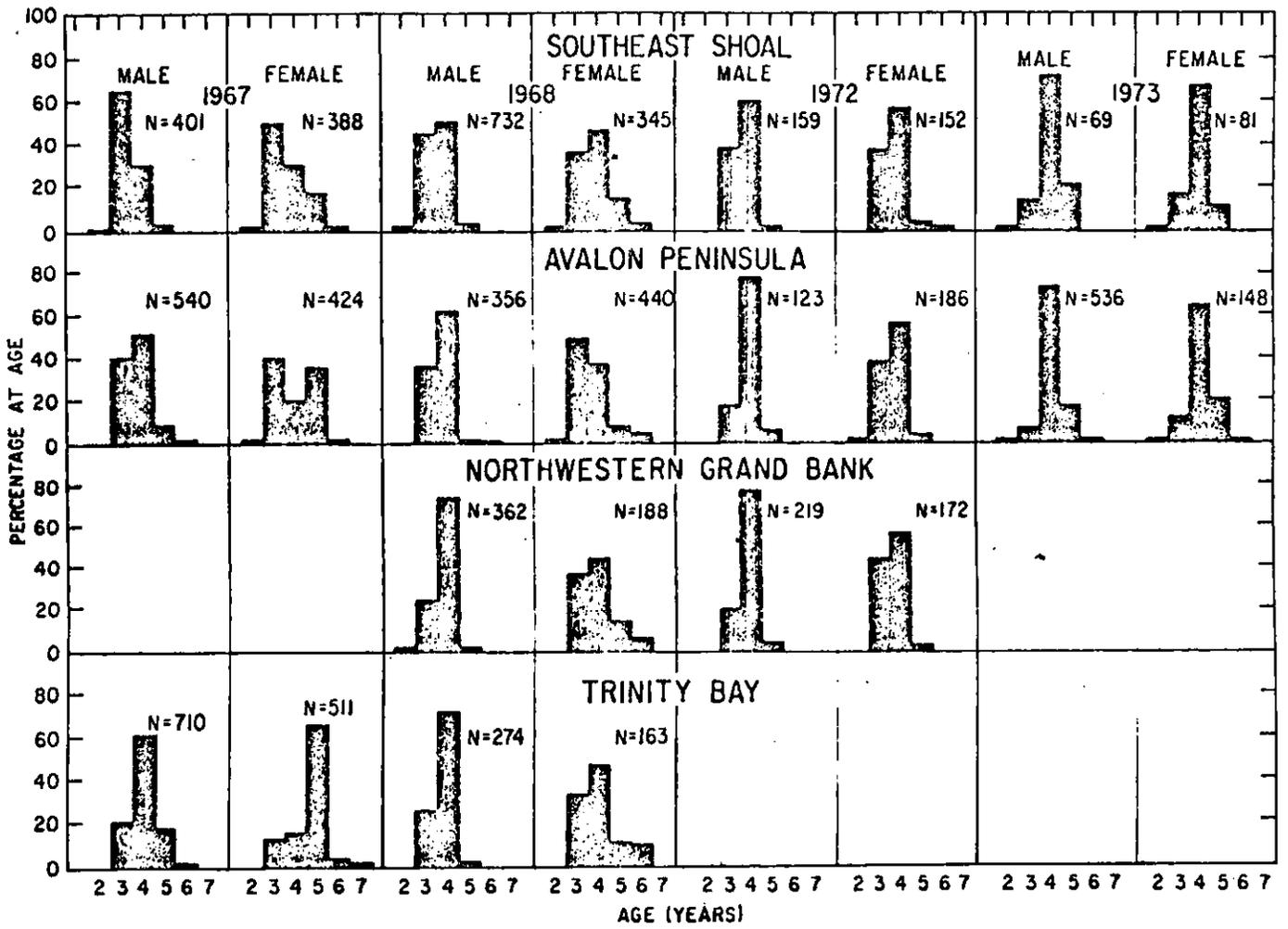


Fig. 5. Age composition of mature capelin from selected areas in Div. 3LNO for the years 1967-68, 1972-73.