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Estimates of the Possible Consumption of Capelin by the Cod Stocks in Divisions 2J+3KL and 3NO

by

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INTRODUCTION

The purpose of this paper is to provide an estimate of the quantity of capelin which might be consumed by the cod stocks in NAFO Div. 2J+3KL and 3NO in 1981. At present there is no information which might help predict the success of cod in locating and consuming capelin under varying levels of cod and capelin abundance and varying hydrographic conditions. Indeed, there is no estimate, based on adequate seasonal and spatial sampling, of the contribution of capelin to the total food consumption of a single cod stock in a given year. However, the broad seasonal patterns of cod predation on capelin have been described, and a few quantitative studies are available. Gross estimates of the consumption of capelin by cod in 1981 may be made, if it be assumed that detailed quantitative information from limited spatial and seasonal sampling may be extrapolated to the whole area on an annual basis, and that predation patterns remain stable from year to year.

The seasonal pattern of cod predation on capelin in 2J3KL, briefly summarized by Akenhead et al. (MS 1981) and Lilly (MS 1981), is similar to the pattern of commercial exploitation of capelin in the mid-1970's (cf. ICNAF, 1975). Predation is apparently most intense on the north slope of the Grand Bank in winter and spring, in the Avalon Channel and on the northwestern Grand Bank in spring, on the northern Grand Bank and inshore all along the coast in late spring and summer, and along the coastal shelfs of 2J3K and on the Hamilton Inlet Bank in late summer and autumn. The predation pattern is highly seasonal in the region of Hamilton Inlet Bank, but much less so on the northern Grand Bank.

Predation by cod on capelin in 3NO appears to be largely confined to spring and summer. Capelin have been reported in cod stomachs in 3O, particularly near the southwest slope, from March to June (Martin and Costa, 1954; Kovalyov and Kudrin, 1973; Bulatova, 1973; Stanek, 1975), and near the Southeast Shoal in 3N in June-July (Martin and Lucio, 1955; Martin, 1956; Templeman, 1965; Bulatova, 1973). These observations correspond with the reported migration of capelin through 3O to the Southeast Shoal, where they spawn in June-July (Kovalyov and Kudrin, 1973). Capelin is a minor component of the cod diet in both 3O and 3N in August, when the major prey is sand lance (Popova, 1962). There appear to be no observations of the food of cod in 3NO during the autumn.

Two methods were used to estimate the probable consumption of capelin by cod in 1981. The first method assumes that published values of the annual consumption of capelin per unit biomass of cod can be applied to the average biomass of cod projected for 1981. The second method involves estimation of the production and total food consumption by cod in 1980-81. A portion of the total consumption is then assigned to capelin on the basis of previous observations of the occurrence of capelin in cod stomachs.

METHODS

CAPELIN CONSUMPTION PER UNIT COD BIOMASS

The projected mean biomass of cod in 1981 was calculated from projected numbers-at-age in 1980 and 1981 (Table 1) and mean weight-at-age in 1979 (Table 2). Projected numbers-at-age for cod in Div. 2J+3KL were calculated using the results of cohort analysis and the assumptions in Wells and Bishop (MS 1980). Numbers-at-age for cod in Div. 3NO are provided by Bishop (MS 1980). The mean number of cod of age i ($\bar{N}_i$) in 1981 was estimated as:

$$\bar{N}_i = \frac{N_{i,1} - N_{i+1,\,2}}{\log_e N_{i,1} - \log_e N_{i+1,\,2}}$$

where $N_{i,1}$ is the projected number at age i at 1 January 1981, and $N_{i,2}$ is the projected number at 1 January 1982. The mean biomass of a cohort in 1981 was calculated as $\bar{N}_i\,\bar{w}_i$, where $\bar{w}_i$ is mean weight at age i. The total mean biomass was estimated by summing $\bar{N}_i\bar{w}_i$ over i.

This estimated mean biomass was applied to published values of capelin consumption per unit cod biomass.

CONSUMPTION ESTIMATED FROM PRODUCTION

The production (P) of cod of specified ages in 2J+3KL and 3NO was estimated as the sum of somatic growth (Ps) and the biomass of reproductive products (Pr). Information available for calculating growth of a cohort was projected numbers-at-age at 1 January 1980-82, and mean weight at age of cod in the commercial fishery in 1979. It was assumed that the mean weight-at-age was appropriate to the mid-point of the year, and population numbers were adjusted to this point.

Thus, the number of cod in a cohort at the midpoints of 1980 and 1981 were calculated from the numbers-at-age on 1 January 1980-82, and the mean number ($\bar{N}_i$) in 1980-81 was calculated as:

$$\bar{N}_i = \frac{N_{i-1,1} - N_{i,2}}{\log_e N_{i-1,1} - \log_e N_{1,2}}$$

where $N_{i,1}$ is the estimated number at age i at midpoint of 1980 and $N_{i,2}$ is estimated number at midpoint 1981. Individual somatic growth ($Ps_i = \Delta\, w_i$) in 1980-81 was estimated as:

$$\Delta\, w_i = \bar{w}_{i,2} - \bar{w}_{i-1,1}$$

where $\bar{w}_{i,1}$ is mean weight at age i in 1980, $\bar{w}_{i,2}$ is mean weight at age in 1981, and $\bar{w}_i$ is assumed to be constant from year to year. The biomass of gonadal products (G_i) in mature fish can often be treated as

$$G_i = a\, w_i^{\,b}$$

where a and b are constants (Bagenal, 1978). The value of b is frequently greater than 1 (MacKinnon, 1972; Ware, 1980), but a simplified formula

$$G_i = 0.1\, w_i$$

may be adequate (Jones and Johnston, 1977; Majkowski and Waiwood, 1980). The approximate proportion mature at age (pM_i) was obtained from Fleming (1960). Reproductive output (Pr_i) is thus $0.1\,\bar{w}_i\,pM_i$. Total individual production (P_i) is $Ps_i + Pr_i$, and total cohort production is $P_i\,\bar{N}_i$.

Consumption (C) was calculated from production by assuming a constant gross growth efficiency (K = P/C) for all ages. Consumption of capelin was calculated as a proportion of total consumption, using published values for the proportion by weight of capelin in total stomach contents of cod.

RESULTS

CAPELIN CONSUMPTION PER UNIT COD BIOMASS

The projected mean biomass of cod of ages 4-13 in Div. 2J+3KL in 1981 is 1,629,000 mt, and the biomass of cod of ages 3-13 in Div. 3NO is 216,000 mt, for a total of 1,845,000 mt (Table 2).

Estimates of the capelin consumption per unit of cod biomass in various areas off Labrador and eastern Newfoundland are provided by Campbell and Winters (1973), Minet and Perodou (1978), Turuk (1978) and Winters and Carscadden (1978).

Campbell and Winters (1973) stated that "from preliminary data collected on the food of cod in Div. 3L, it appears that, on the average, cod consume from 0.5 to 1.0 times their weight in capelin annually." The derivation of this consumption rate is not given. Winters and Carscadden (1978) estimated the annual consumption of capelin per unit weight of cod in unexploited cod stocks by assuming that for a population in equilibrium, the production-biomass ratio (P/B) is equal to the total mortality coefficient (Z). Since consumption (C) may be calculated from P/K, where K is gross growth efficiency, then consumption may be estimated as

$$C = P/K = BZ/K.$$

Consumption of capelin per unit biomass of cod is

$$C/B = (Pc\ BZ)/(KB),$$

where Pc is the proportion of capelin in the cod diet. By assuming Pc = 0.32 (Campbell and Winters, 1973), Z = 0.2, and K = 0.1, Winters and Carscadden (1978) calculated that the annual consumption of capelin per unit weight of cod was 0.64, They then assumed, however, that at the reduced level of cod abundance in the late 1960's the upper limit of the range given by Campbell and Winters (1973) (i.e. 1.0) might be more applicable.

Minet and Perodou (1978) used a more direct method of estimatng consumption rates of cod in 2J3KL. They assumed that cod ate in discrete meals, and estimated from empirical data the mean weight of capelin in the meal of an average cod. From published information on gastric evacuation rate, they calculated the number of meals of capelin per year, assuming as well that cod prey on capelin for only half of the year (summer and winter), and concluded that the average cod consumed from 0.76 to 1.27 times its weight of capelin annually. This range was considered a minimum estimate, since there would be some predation by cod on capelin in spring and autumn, and the intense inshore predation in summer was not included in the sampling.

Turuk (1978) also used a direct method. She combined estimates of feeding rate with observations on stomach contents for cod in Subarea 2 and Div. 3NO. The daily feeding rates of cod in 2GHJ and 3NO were stated to be 3.17% and 7.28% of body mass respectively (source unstated). The period of intensive predation was reported to be 4 months (August-November) in 2GHJ and 3 months (May-July) in 3NO. Turuk apparently assumed that during these periods the cod fed entirely on capelin, and thereby calculated that the minimum annual consumption of capelin by cod was 3.8 times the cod biomass in 2GHJ and 6.5 times cod biomass in 3NO. However, the frequency of occurrence of capelin in cod stomachs containing food was only 65% off Labrador and 35% in 3NO. Turuk indicated that these values should be used to correct the above estimates of capelin consumption. Such a correction is inappropriate, since it uses percent occurrence rather than percent weight, but when applied it yields values of 2.47 and 2.29 for the weight of capelin eaten per unit weight of cod in 2GHJ and 3NO respectively. (Note that Turuk did not make this change correctly in her Table 2). The average of these 2 values is 2.38.

Assuming that the estimates by Minet and Perodou (1978) for 2J3KL are applicable to the 3NO cod stock, and the average of the estimates by Turuk (1978) for 2GHJ and 3NO is applicable to both 2J3KL and 3NO, then the estimates of the consumption of capelin per unit biomass of cod range from 0.8 to 2.38. Thus, for a projected cod biomass in 1981 of 1845 x 10^3 mt, the estimated consumption of capelin by cod is 1402-4391 x 10^3 mt.

CONSUMPTION ESTIMATED FROM PRODUCTION

Population production in 1980-81 by cod aged 5-13 in the 2J3KL cod stock was estimated to be 688 x 10^3 mt (Table 3), and production by ages 4-13 in the 3NO cod stock was estimated to be 82 x 10^3 mt (Table 4), for a total of 770 x 10^3 mt. The gross growth efficiency of the cod is not known, but assuming it lies between 0.1 and 0.2, then the total food consumption of cod in 2J3KL and 3NO in 1980-81 is 3850 - 7701 x 10^3 mt (Tables 3 and 4).

The proportion of capelin in the diet of cod on a broad seasonal and areal basis has not been investigated, but observations from limited spatial and seasonal coverage are available. Templeman (1965) reported that capelin comprised 55% by volume of the food of cod taken from May to November in the inshore fishery at St. John's. Campbell and Winters (1973) estimated that capelin comprised 32% of the food of cod on an annual basis. The times and places of sampling were not stated. Minet and Perodou (1978) found that capelin comprised 56% of the diet of cod in 2J3KL during the winter and summer feeding periods. By assuming that no capelin are consumed during spring and autumn, they projected a corresponding figure of 28% on an annual basis. However, they cautioned that this would be a minimal figure for the reasons summarized above.

If it be assumed that capelin comprise about 30% of the cod diet, then consumption of capelin by cod in 2J3KL and 3NO in 1980-81 would be 1155 - 2310 x 10^3 mt. If the estimate of 56% calculated by Minet and Perodou (1978) is reduced by 0.25 (to 42%) rather than by 0.5 (to 28%) to allow for predation in areas and times not covered by their sampling, then consumption of capelin would be 1617 - 3234 x 10^3 mt.

The various estimates of the quantity of capelin which might be consumed by cod in 1981 (or 1980-81) are summarized below.

For a biomass of 1845 x 10^3 mt of cod

Authority	Capelin consumed per unit cod biomass	Capelin consumed (x10^{-3} mt)
Winters and Carscadden (1978)	1.0	1845
Minet and Perodou (1978)	0.76	1402
	1.27	2343
Turuk (1978)	2.38	4391

For a production of 770 x 10^3 mt

Percent capelin	K		Capelin consumed (x 10^{-3} mt)
30	0.2		1155
	0.1		2310
		average	1733
42	0.2		1617
	0.1		3234
		average	2426

DISCUSSION

There are two basic ways of estimating the quantity of a given prey consumed by a predator. A direct method is to measure the quantity of that prey in the stomachs of the predators, and to estimate feeding rate by applying estimates of the rate of passage of the prey through the predator's gut. An indirect method is to estimate consumption from a metabolic model and empirical data on production, and to assign a portion of the total consumption to the prey under consideration on the basis of that prey's contribution to the total stomach contents of the predator. Both methods require quantitative observations of the predator's stomach contents on a seasonal basis throughout the predator's entire range.

In their studies of capelin consumption by cod, Minet and Peredou (1978) and Turuk (1978) used a direct method, whereas Winters and Carscadden (1978) used an indirect method. A major limitation of all three studies is that they have not involved the extensive sampling required to encompass all feeding patterns by the cod as it moves seasonally through the heterogenous physical and biotic environment off eastern Newfoundland and Labrador. The methods of Minet and Perodou (1978) were insightful, but they were obviously hampered by inadequate information on gastric evacuation rate. The estimates by Turuk (1978) cannot be evaluated, for they involve feeding rates which are not derived within her paper.

The indirect method used by Winters and Carscadden (1978) and in the present paper involves considerable uncertainty. Estimates of total production can be considerably improved by more accurate measures of the quantity of reproductive products released, especially if such measures are in terms of energy rather than weight. The present estimate (0.1 w) may yield minimum values (Jones and Johnston, 1977). Use of a bioenergetics model (e.g. Kitchell, Stewart and Weiniger, 1977) to estimate consumption would permit exploration of the various factors which might affect consumption, but parameter estimation for cod seemed a difficult problem, especially at the low temperatures prevailing in the study area. It was therefore decided to use gross growth efficiency to estimate consumption from production. The value of 0.1 used by Winters and Carscadden (1978) may be low, for gross growth efficiencies as high as 0.24 have been found in laboratory experiments (Edwards, Finlayson and Steele, 1972). Growth efficiencies tend to decline with body size, but vary widely in response to many other variables, including feeding rate, prey size and temperature (see review by Conover, 1978). Majkowski and Waiwood (MS 1980) used empirical cod growth data and physiological parameters to estimate consumption by cod in the southern Gulf of St. Lawrence, and calculated gross growth efficiencies declining from 0.23 in cod of age 1 to about 0.10 in cod of age 7+. In the present paper values of 0.1 and 0.2 were chosen to span the probable range. As discussed above, the contribution of capelin to the total food consumption of cod is poorly known, but this too is an important factor in the calculation, for a change from 30% to 40% increases the estimate of capelin consumption by a third. When more extensive information is available, it will be necessary to vary this factor with the size (or age) of cod, for Lilly and Fleming (MS 1980) found that the importance of capelin varied with cod size, being maximal at cod lengths of 40 to 70 cm.

The present estimates of capelin consumption by cod, based on projected production in 1980-81, vary from 1155 to 3234 x 10^3 mt. It is not possible with present information to suggest which estimate is most appropriate. Published values of capelin consumption per unit weight of cod range from 0.76-1.27 (Minet and Perodou, 1978) to 2.38 (Turuk, 1978). When these values are applied to the cod biomass projected for 1981, they yield estimates of capelin consumption by cod ranging from 1402 to 4391 x 10^3 mt. Both Minet and Perodou (1978) and Turuk (1978) cautioned that their estimates may be minimim values. However, both studies were conducted in the mid-1970's (Turuk in 1973-76; Minet and Perodou in 1975-76), at which time the cod biomass was very low (Bishop, MS 1980; Wells and Bishop, MS 1980) and the capelin biomass was high, particularly in 1975-76 as a result of the large 1973 year-class (Carscadden and Miller, MS 1980). Thus, at the time of the cod feeding studies the quantity of capelin available per unit biomass of cod was probably considerably greater than at present and may have been at the highest levels for many years.

The only comparable data from other areas where cod prey on capelin are provided by Ponomarenko, Ponomarenko and Yaragina (MS 1978), who used a method similar to that of Turuk (1978) and estimated that in 1974-76 cod in the Barents Sea consumed annually a biomass of capelin equal to 2.4-2.7 times their own biomass. Ponomarenko and Yaragina (MS 1978) reported that the annual frequency of occurrence of capelin in the stomachs of cod from the Barents Sea fluctuated considerably between 1947 and 1976, apparently in response to changes in abundance of mature capelin.

It is emphasized that studies of the flow of energy (or matter) between two species describe only the situation at the time of observation, and have little if any predictive power. There is as yet no evidence that cod and capelin are strongly linked (Akenhead et al., MS 1981), and if the linkage is in reality weak, then the present estimates of the quantity of capelin which might be consumed by cod cannot be equated to the quantity of capelin required by cod. Akenhead et al. (MS 1981) discuss briefly the possibility that other species, both pelagic and benthic, may provide adequate forage for cod during periods of reduced capelin abundance. An interesting example is the predation in recent years by Atlantic cod on Arctic cod (Boreogadus saida) in 2J, 3K and northwestern 3L (unpublished data). Arctic cod have never before been reported from cod stomachs in this area. Clearly, future research must consider not only the nutritional quality of various potential prey and the ability of the cod to switch from one prey to another, but also the response of the whole ecosystem to changes in the abundance of a numerically important species such as capelin.

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Table 1. Projected numbers-at-age (x 10^{-5}) of cod on 1 January 1980-82. Projections for 2J3KL were based on methods and assumptions in Wells and Bishop (MS 1980). Projections for 3NO are provided by Bishop (MS 1980).

	Age	1980	1981	1982
2J3KL	4	1250	1250	-
	5	3320	996	993
	6	3027	2490	738
	7	1889	2221	1799
	8	550	1344	1550
	9	155	384	919
	10	53	106	257
	11	28	36	71
	12	20	19	24
	13	8	13	12
	14		5	9
3NO	3	250.0	400.0	-
	4	147.5	202.7	324.2
	5	372.3	113.7	156.3
	6	311.4	265.0	81.0
	7	70.3	212.9	181.2
	8	27.6	48.1	145.6
	9	12.4	18.9	32.9
	10	4.5	8.6	13.2
	11	2.6	3.2	6.1
	12	2.1	2.1	2.5
	13	1.0	1.6	1.6
	14	1.0	0.8	1.3

Table 2. Projected mean biomass of cod in 1981 in 2J3KL and 3NO.

	Age	Mean weight (kg)	Mean number (x 10^{-5})	Mean biomass (MT x 10^{-3})
2J3KL	4	0.74	1117	82.6
	5	1.12	861	96.4
	6	1.68	2126	357.1
	7	2.49	1865	464.5
	8	3.60	1118	402.5
	9	4.46	316	141.1
	10	5.31	87	46.4
	11	5.86	30	17.3
	12	7.18	15	10.9
	13	9.02	11	9.8
	Total			1628.7
3NO	3	0.72	360	26.0
	4	1.05	178	18.7
	5	1.55	96	14.9
	6	2.25	220	49.6
	7	3.74	177	66.3
	8	4.61	40	18.4
	9	6.19	16	9.8
	10	7.23	7	5.3
	11	9.48	3	2.7
	12	12.87	2	2.3
	13	15.38	1	2.2
	Total			216.3
Total: 2J3KL + 3NO				1845.0

Table 3. Estimated production and food consumption by cod in Divisions 2J 3KL in 1980-81. (Ps and Pr are individual somatic and reproductive growth respectively; $\bar{w}$ is mean weight in 1981; pM is proportion mature; $\bar{N}$ is average number from midpoint 1980 to midpoint 1981).

Age in 1981	Ps (kg)	$\bar{w}$ (kg)	pM	Pr (kg)	$\bar{N}$ ($\times 10^{-5}$)	Population production (m tons $\times 10^{-3}$)	Population consumption (m tons $\times 10^{-3}$) K=0.2	K=0.1
5	0.38	1.12	0.10	0.01	984	38.4	191.8	383.7
6	0.56	1.68	0.50	0.08	2486	159.1	795.6	1591.2
7	0.81	2.49	0.75	0.19	2214	221.4	1106.9	2213.9
8	1.11	3.60	0.90	0.32	1345	192.4	961.8	1923.6
9	0.86	4.46	1.00	0.45	385	50.4	251.9	503.8
10	0.85	5.31	1.00	0.53	107	14.7	73.7	147.4
11	0.55	5.86	1.00	0.59	36	4.1	20.7	41.4
12	1.32	7.18	1.00	0.72	19	3.9	19.3	38.6
13	1.84	9.02	1.00	0.90	13	3.7	18.3	36.7
Total						688.0	3440.0	6880.1

Table 4. Estimated production and food consumption by cod in Divisions 3NO in 1980-81. (Ps and Pr are individual somatic and reproductive growth respectively; $\bar{w}$ is mean weight in 1981; pM is proportion mature; $\bar{N}$ is average number from midpoint 1980 to midpoint 1981).

Age in 1981	Ps (kg)	$\bar{w}$ (kg)	pM	Pr (kg)	$\bar{N}$ ($\times 10^{-5}$)	Population production (m tons $\times 10^{-3}$)	Population consumption (m tons $\times 10^{-3}$) K=0.2	K=0.1
4	0.33	1.05	0	0	201	6.6	33.1	66.2
5	0.50	1.55	0.05	0.01	112	5.7	28.4	56.8
6	0.70	2.25	0.20	0.05	264	19.7	98.3	196.5
7	1.49	3.74	0.50	0.19	214	35.9	179.6	359.3
8	0.87	4.61	0.75	0.35	48	5.9	29.4	58.8
9	1.58	6.19	0.90	0.56	19	4.1	20.4	40.8
10	1.04	7.23	1.00	0.72	9	1.5	7.7	15.4
11	2.25	9.48	1.00	0.95	3	1.1	5.3	10.5
12	3.39	12.87	1.00	1.29	2	1.0	4.8	9.6
13	2.51	15.38	1.00	1.54	2	0.7	3.3	6.6
Total						82.0	410.2	820.4