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Estimates of herring consumption by cod in 4T -

A preliminary analysis of current and historical data

by

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[1] This series documents the scientific basis for fisheries management advice in Atlantic Canada. As such, it addresses the issues of the day in the timeframes required and the Research Documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Abstract

The percent occurrence of herring in the diet of Gulf of St. Lawrence cod and the geographic and seasonal patterns of herring predation by cod are presented for the periods 1959-73 and 1980-81. Using a consumption model, estimates of the dietary fraction attributable to herring, cod numbers-at-age from SPA, and the total and herring food biomass eaten by cod age groups 3 to 13 was calculated for the above time series in a defined area and season. Predation on herring appeared most intense during the summer to early fall months in the Shediac Valley-Miscou Bank area. Herring was not a major food component of cod younger than 8 years ($\gtrsim$70 cm). Year to year variation in herring predation was substantial with high levels estimated for the early and late 1960's and low levels in the most current years. Herring biomass consumed by cod was positively correlated with 2 + 3 year-old herring biomass during the years 1969-73 and 1979-80.

Résumé

Nous décrivons dans l'article qui suit l'incidence de hareng, en pourcentage, dans la diète de la morue du golfe du Saint-Laurent, ainsi que les caractéristiques géographiques et saisonnières de la prédation exercée par la morue sur le hareng durant les périodes 1959-73 et 1980-81. A l'aide d'un modèle de consommation, nous avons estimé, pour ces périodes, la fraction du régime alimentaire attribuable au hareng, le nombre de morues par âge découlant d'une analyse séquentielle de population et la biomasse totale et celle du hareng ingéré par la morue des groupes d'âge 3 à 13, dans une aire et pendant une saison définies. La prédation sur le hareng semble maximale pendant les mois d'été et début d'automne dans la région de la vallée de Shédiac-banc de Miscou. Le hareng n'est pas un élément majeur du régime des morues âgées de moins de 8 ans ($\gtrsim$70 cm). La prédation sur le hareng varie beaucoup d'une année à l'autre, les hauts niveaux se trouvant au début et à la fin des années 1960, et les bas niveaux durant la période la plus récente. Il y a corrélation positive entre la biomasse de hareng consommé par la morue et celle des harengs de 2 et 3 ans dans les années 1969-73 et 1979-80.

Introduction

Previous investigations on gadoid predation in various ecosystems have shown that significant consumption of commercially important prey does occur and that this may approach or surpass the biomass taken by the fisheries themselves (Daan 1973, 1975, Minet and Perdou 1978, Ponomarenko et al. 1978). Laevastu and Favorite (1977, 1978) have suggested that a high walleye pollock (*Theragra chalcogramma*) biomass has contributed to the disappearance of the shrimp resource and has suppressed the herring resource in the eastern Bering Sea. A parallel situation may have existed between cod and brown shrimp (*Crangon crangon*) in the North Sea during the early 1970's (Boddeke in Daan 1973).

In the southern Gulf of St. Lawrence (NAFO Div. 4T), cod represent the major groundfish fishery with recent catches of about 40,000 tons (Sinclair and Maguire 1981). Previous studies by Corbeil (1953), Powles (1958), Kohler (1964), and Kohler and Fitzgerald (1969) have shown that herring contribute a significant portion of the diet of 4T cod. Unfortunately, evaluation of the annual biomass of herring eaten by cod in the southern Gulf has not been possible due to the lack of feeding data throughout the year. However, cod stomach analysis has been conducted on fall groundfish surveys in the southern Gulf of St. Lawrence during the years 1959-73 and 1979-81, and additional studies were conducted during the summers of 1979 and 1980 (Waiwood et al. 1980, Waiwood 1981. The purpose of this paper is to determine whether these data can contribute to our understanding of herring predation in the south-western Gulf of St. Lawrence. Specifically, we have considered: patterns of herring predation related to location, season and cod size, whether year to year estimates of herring predation (during a restricted period and in a defined area) reflect the biomass of herring susceptible to predation, and whether meaningful yearly estimates of herring predation by cod can be made.

Methods

Stomach content analysis. Estimates of year to year variation in the dietary contribution of herring were based on cod stomach content data collected on fall groundfish surveys during the years 1959-73 and 1979-81. The locations of sampling stations are given in Fig. 1. Since the area surveyed during 1964-68 was more restricted than in other years, an area of 9500 km^2 was defined for all years (Fig. 1) which corresponded to this restricted area. Of the 25,834 stomachs analyzed in the time series, 14,439 were from the defined area. Details of sampling are given in Table 1.

On board stomach analysis, conducted during 1959-73 and in 1979, was relatively crude when compared to that done with preserved material (1980-81). However, it was assumed that measurements based on either method gave similar results. In all cases, the percentage dietary contribution of herring was adjusted by assuming that the composition of unidentified fish remains was identical to that of the identified fraction (Waiwood and Elner, 1982). Empty stomachs were excluded from the analysis.

The average percentage dietary contribution of herring was calculated for different size categories of cod, each representing a specific age grouping. These size categories spanned the midpoints (between ages) in the weight-at-age matrix. Size categories representing ages 9-10 and 11-15 were combined.

Consumption model

The procedure used to evaluate the food biomass consumed by cod of different age-groups was based on an application of Ursin growth theory (Ursin, 1967, 1979; Andersen and Ursin, 1977; Andersen et al. 1973) which relates food consumption to growth. The model uses empirical growth data for cod, values for the required physiological parameters and the appropriate numbers-at-age. Since the description and reliability of the procedure have been presented previously (Majkowski and Waiwood 1980, 1981), they will not be described here. Values for the physiological input parameters used in the model are presented in Table 2. Weights-at-age for the years 1959-73, and 1979-81 are given in Table 3 and are from Beacham (1980) and Sinclair and Maguire (1981).

The average numbers-at-age $\bar{N}_i$ for each year were calculated using the following equation from Ricker (1975):

$$\bar{N}_i = \frac{N_{oi}(1-e^{Z_i})}{Z_i} \qquad (1)$$

where Z_i was the sum of F_i (Table 10C in Sinclair and Maguire 1981) and M_i which was given the value of 0.2 for all ages and years. The starting numbers-at-age N_{oi} were taken from Sinclair and Maguire (1981). The computed values for $\bar{N}_i$ are given in Table 4.

The biomass of food consumed by cod in area 4T (R_{4Ti}) was calculated as the yearly food biomass minus the biomass of food eaten in area 4Vn (R_{4Vn}) where the latter value was estimated to equal one third the yearly maintenance ration (see Majkowski and Waiwood 1980, 1981). The biomass of herring eaten by cod during September of each year (R_{Hi}) and in the defined area was calculated using the following equation:

$$R_{Hi} = pqr_i \, \bar{N}_i R_{4Ti} \qquad (2)$$

where p (= 0.125) was the fraction of the time spent in 4T represented by the month of September, q (= 0.35) was the fraction of the population inhabiting the defined area (Waiwood et al. 1980), r_i was the fraction of the food biomass represented by herring, $\bar{N}_i$ was the yearly average numbers-at-age (Table 4) and R_{4Ti} was the average food biomass eaten in 4T by cod of the i-th age. No corrections were made to adjust for monthly differences in consumption or for year to year variation in September consumption.

Results

Contribution of herring in the cod diet

Seasonal and geographic variation. Figure 2 shows the geographic distribution of herring predation by cod in the southern Gulf of St. Lawrence for the years 1959-73, 1980-81. Although data from the overwintering area (Sydney Bight) are not included in the January to March period, a general pattern emerges for the early spring to late fall period. In the late spring, cod predation on herring was restricted to the slope edge along the Laurentian channel and in the area off Gaspé. During the summer and early fall, predation on herring was almost completely restricted to the Shediac Valley, Bay of Chaleur, Gaspé and American Bank regions.

In the late fall and early winter, herring predation was more generally distributed in the Gulf. These data suggest that the seasonal and geographic pattern of herring predation by cod seem to coincide with the concurrent migration patterns of the two species. In any case, for the period July to September, maximum herring predation appears to occur within the defined area indicated in Fig. 1.

Year to year variation in herring predation. Table 5 shows the calculated fractions of the cod diet attributable to herring for September during the years 1959-73, 1979-81. The highest dietary levels of herring occurred in the early 1960's and late 1960's early 1970's. Herring was virtually non-existent in the diet of cod in 1979-81 (September). The level of herring in the diet of cod <7 years was relatively low with the highest levels recorded in cod 11-15 years.

Total food consumption

Yearly consumption-at-age estimates for 3-15 year-old cod as generated by the analysis are given in Table 6. Due to inconsistent weight-at-age estimates for some years (marked by asterisks), averages for the corresponding ages were substituted for the generated values. The food biomass eaten by cod increased greatly with increasing cod size, although the consumption relative to body weight was higher for younger (smaller) than for older cod. For example, 3-year-old cod consumed approximately 2.5 times their weight annually while the corresponding value for 11+ cod was about 1.4 times. The individual biomass of food eaten in 4T by cod ages 3-15 are shown in Table 7. These values were multiplied by the average yearly numbers-at-age and adjusted to correspond to the defined area and period to yield the corresponding biomass of food eaten by age-groups 3-15 (Table 8). The September consumption of herring by cod age-groups 3-15 for the years 1959-73 and 1979-81 was estimated as the product of the dietary fraction (Table 5), and the adjusted age-group consumption (Table 8). These values are displayed in Table 9.

It is quite apparent that total food consumption by age-groups is more greatly influenced by the numbers-at-age than by the consumption-at-age values. Except for the late 1950's and early 1960's, little herring was consumed by age-groups 3 and 4. With the possible exception of the period 1964-69, relatively little herring was consumed by 11+ cod age-groups, again, a function of their small numbers. The highest levels of herring consumption (September) occurred in 1959 and 1960. Extremely low levels were calculated for 1979 and 1981 with only 29 and 7 tons being consumed respectively in the September of these years (Table 9). The ratios of herring food biomass to total food biomass (x100) for the time series are shown in Table 10. Over the 18 years, herring biomass accounted for an average of 6.8% of the total food biomass (range, 0.02-12.1%).

Herring consumption and herring biomass. Virtually no data exist for 4T to describe the predator-prey size relationship between cod and herring. According to Daan (1973), only herring less than about 20 cm were consumed by cod. On this basis, we have compared the herring biomass eaten by cod to the biomass estimates for 2- and 3-year-old herring. SPA analysis from Cleary (1981) was used to represent the latter and hence only 7 points (1969-73, 1979-80) could be plotted. Herring biomass consumed was positively correlated with 2 + 3 year old herring biomass (Fig. 3). The corresponding regression with 2-4 herring biomass (Fig. 4) had a higher r^2 (0.88) while that for age 2 biomass alone (Y (tons) = 8057 + 9.85 X) had a lower r^2 (0.74).

The contribution of herring to the total food biomass of cod appeared to increase with increasing herring biomass (Fig. 5). Hence, at higher levels of 2 + 3 year old herring biomass, the ratio of herring food biomass to the total food biomass of cod was higher than at lower levels of herring population biomass.

Discussion

The data presented here suggest that the occurrence of herring in the diet of 4T cod reflects the seasonal distributions of the two species and that herring predation is concentrated in the Gaspé-Shediac Valley-Miscou Bank area during the summer months. Powles (1958) also showed significant levels of herring in the diet of cod from this area and that the dietary level of herring increased over the period June to August.

Generally, herring was not a major food component of cod younger than 8 years (≈ 70 cm). The relatively high levels in 5-7 year-old cod during 1959 and 1960 (Table 5) may reflect the large herring year classes of 1958 and 1959. During the mid 1950's, the high incidence of herring in the diet of cod less than 50 cm (Corbeil 1953, Powles 1958) was probably related to the outbreak of an epizootic disease *Ichthyosporidium hoferi* which left herring highly vulnerable to predation (Kohler 1964).

Estimates of yearly consumption-at-age generated by our analysis are at the lower end of the range reported in the literature. However, when allowances are made for ambient temperature, our values are well within the range reported by Daan (1975) and Grosslein et al. (1980).

Evidence is presented here to suggest that year to year variation in the biomass of herring eaten by cod can be attributed to changes in the herring biomass. The highest levels of herring consumption, in the time series (1959 and 1960), are undoubtedly related to the very large herring year-classes of 1958 and 1959. These supported the herring fishery for over 10 years.

The relationship in Fig. 5 indicates that the percent of the total food biomass (eaten by 3-15 year-old cod) attributable to herring is not constant over a wide range of herring biomass. At very low levels of herring biomass, herring accounted for less than 1% of the total food biomass. On the other hand, the biomass of herring eaten by cod never exceeded 12% of the total food biomass.

From the data presented here, it is not possible to calculate accurate estimates of the yearly consumption of herring by cod. However, during periods of low herring biomass, it is unlikely that herring contribute more than 6% of the total food biomass of 3+ cod.

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Table 1. Details of stomach sampling and analysis used to determine year to year variation in the contribution of herring in the diet of 4T cod during September of each year.

Period	Method of analysis	Unit	Sampling design	No. stomachs* analyzed (defined area)
1959-1969	on board	% by volume	fixed stations	9,425
1970-73 and 1979	on board	% by volume	fixed + stratified random stations	3,226
1980-1981	laboratory	% by weight	same as above	1,718

*excluding empty stomachs.

Table 2. Physiological parameters used in the calculations of food consumption rates of cod.

Symbol	Explanation	Value	Unit	References
β_i	Assimilated fraction of consumed food	0.8	Pure number	Winberg (1956); Ursin (1967, 1979)
α_i	Fraction of assimilated food lost in feeding catabolism	0.4	Pure number	Ursin (1967, 1979); Andersen & Ursin (1977)
k_i	Coefficient of the term for fasting catabolism	1.9	g^{1-n_i}/years	Waiwood & Majkowski (unpublished data)
n_i	Exponent of the term for fasting catabolism	0.83	Pure number	Ursin (1979)
m_i	Power value of the term relating the food consumption rate to the body weight	0.56	Pure number	Andersen & Ursin (1977)
a	Coefficient of the formula relating the biomassed reproductive products spawned by a cod during the year to its body weight	0.0512	g^{1-b}	Waiwood & Majkowski (unpublished data)
b	Power value of the formula relating the biomass of reproductive products spawned by a cod during the year to its body weight	1.145	Pure number	Waiwood & Majkowski (unpublished data)
pi	Fraction of mature cod at		Pure number	Beacham (pers. comm.)
	age 3	.17		
	4	.66		
	5-15	1.0		

Table 3. Weight-at-age values of cod ages 2-15 for various years. These values were used in estimation of food consumption and are taken from Beacham (1980). Weights-at-age for 1980 were taken from Waiwood and Majkowski (in preparation). Weights-at-age as estimated from the 1980 overall fishery were used to approximate values for 1981 (Sinclair and Maguire 1981). Values for ages 2 and 3 were taken from R.V. data.

	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	78	79	80	81
2	140	140	170	150	190	190	190	220	170	200	190	180	180	130	150	170	170	110	110	110
3	360	360	340	300	630	370	390	400	370	440	420	430	420	420	390	330	330	250	350	540
4	990	850	840	840	670	600	630	770	640	860	620	830	740	750	470	690	600	650	770	690
5	1420	1240	1110	1030	950	840	810	880	1170	1350	1090	1280	990	1130	900	1010	860	980	990	900
6	1880	1660	1650	1410	1240	1080	1050	1060	1200	1560	1510	1690	1380	1340	1360	1290	1490	1370	1230	1200
7	2540	2120	2200	1930	1730	1350	1340	1410	1490	2420	2140	2500	2110	1940	1490	1730	2190	1890	1500	1510
8	3160	2870	2880	2680	2340	2000	1780	1730	1950	1490	2750	3520	3780	3070	2170	2100	2590	2400	2730	2650
9	3830	3660	4180	4510	3060	3170	2530	2410	2440	2740	2800	3140	2070	3690	4140	2580	3870	3370	4140	3130
10	4750	3840	3760	4330	4290	4970	4560	3390	3480	5220	3790	3360	2790	3580	4360	4640	4240	6740	2750	4150
11	5250	5050	5770	5370	6640	5250	7540	5690	5540	3620	3890	4960	5720	8900	5830	5050	4770	2910	5570	8270
12	8740	7010	5930	5660	5180	9120	7200	7440	6610	6810	4690	5550	3510	11950	4340	9570	5990	4740	6050	6400
13	6870	11950	8490	8670	9110	5660	11840	10740	8850	8250	7460	7510	7230	3530	5780	4080	3470	5150	9840	11110
14	7040	13100	5730	8820	14340	12650	8430	16710	11460	10570	7720	3140	9850	9490	5730	7110	7550	5650	10520	5520
15	8610	8610	9850	10000	15650	17550	12360	11390	7830	11600	10630	14340	7150	8020	3450	4890	8020	13850	7690	10100

Table 4. Average numbers-at-age ($\bar{N}i$:) calculated using equation (1) (see text for details.)

	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	79	80	81
3	128454	120846	41249	53716	37017	54357	46661	54228	94209	84632	50487	45896	65851	27531	37737	14032	239161	71124
4	79281	102982	97320	32936	42941	29724	41747	34482	40252	72810	66755	39523	36366	46682	19699	127341	115818	194126
5	56869	59003	75740	72918	24077	30895	20827	26415	22606	25973	49948	44983	27268	22843	26353	74324	95205	87417
6	26806	36450	39851	55404	47067	14926	17705	12283	15114	13902	16243	29716	26319	15650	11202	52868	47782	65408
7	10577	14659	20593	24805	37008	25927	7548	9179	6701	9057	8248	9685	16508	13503	7652	9906	34068	30684
8	6144	4656	7882	11404	13856	19698	11977	3521	5283	3655	5152	4767	4952	8381	6048	4882	5889	21877
9	8188	2225	2735	4645	5978	6889	9622	5488	1973	3256	2012	2625	2511	2346	3766	2417	2885	3781
10	3394	3145	1246	1626	2711	3097	3232	4804	3086	1228	1957	895	1312	1198	1002	1370	1429	1853
11	1811	934	1501	746	896	1657	1554	1488	2732	1650	727	994	389	612	505	287	861	917
12	1150	673	400	854	479	505	997	710	688	1516	863	305	351	190	269	177	132	553
13	431	482	341	173	576	285	275	525	354	274	821	469	106	92	73	66	103	85
14	320	154	271	196	108	386	166	128	295	147	104	486	239	53	22	104	32	66
15	207	121	74	139	124	61	215	93	64	175	61	48	267	118	23	44	71	21

Table 5. Fraction of September cod diet attributable to herring. Values were adjusted to account for the unidentified fish fraction.

	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	79	80	81
3	0.013	0.014	0.000	0.028	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4	0.061	0.020	0.010	0.040	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000
5	0.096	0.041	0.000	0.041	0.000	0.000	0.000	0.000	0.029	0.000	0.012	0.000	0.000	0.000	0.013	0.000	0.000	0.000
6	0.116	0.098	0.110	0.050	0.000	0.000	0.018	0.000	0.010	0.023	0.041	0.047	0.011	0.000	0.021	0.000	0.000	0.000
7	0.151	0.383	0.260	0.112	0.000	0.078	0.000	0.000	0.000	0.045	0.187	0.174	0.066	0.000	0.018	0.000	0.027	0.002
8	0.274	0.302	0.089	0.288	0.093	0.043	0.023	0.039	0.000	0.113	0.196	0.420	0.223	0.075	0.033	0.000	0.028	0.000
9 - 10	0.274	0.206	0.214	0.333	0.266	0.397	0.285	0.393	0.040	0.310	0.469	0.420	0.385	0.366	0.159	0.000	0.110	0.000
11+	0.383	0.000	0.000	0.014	0.000	0.267	0.265	0.577	0.586	0.520	0.622	0.535	0.105	0.134	0.280	0.156	0.000	0.000

Table 6. Individual yearly food biomass (g) consumed by 4VTn cod (ages 3-15) for given years. These values were calculated from the consumption model (see text). Values indicated with an asterick are averages for the corresponding ages.

	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	79	80	81
3	870	825	733	1476	893	939	961	893	1052	1007	1029	1007	1007	939	802	618	848	1276
4	2396	2356	2418	1866	1905	1520	1996	1481	2404	1313	2142	1775	1839	1905	1693	1702	1780	1800
5	2359	2210	1951	1674	1651	1699	1884	2613	3647	2118	3429	1833	2539	1690	2795	2326	2238	1647
6	2886	3245	2691	2273	1891	2021	2122	2463	3085	2524	3743	2231	2713	2474	2741	3132	2403	2220
7	3477	4229	3318	3147	2210	2512	2825	3088	6211	4246	5674	3848	3953	2477	3257	3526	2593	2777
8	4610	5564	4692	4116	3386	3454	3301	3919	2179	4460	4047*	4047*	6262	3520	4267	3771	5695	6260
9	5944	8397	9559	4951	6075	4615	4693	4916	5465	6855	5071	4914*	4790	7785	4416	6202	6905	5080
10	6146	7825	9304	6272	8258	6925	5904	6235	8477	8349	5315	5789*	4686	8063	6649	10049	7988	6186
11	7453	10449	10744	8613	8580	9965	8475	8606	6588	8494	6999	7134*	9397	9847	7066	5620	9163	10242
12	9452	10648	11132	7181	12751	9631	10291	9762	10235	9617	7592	8210*	11856	8038	11376	7836	9711	8458
13	14150	13689	14937	10931	9045	14036	13537	12079	11760	13198	9493	9256*	4639	9788	6068	8303	13791	12850
14	15203	10400	15118	15603	16292	10830	19099	14662	14126	13516	5071	10504*	9838	9729	9083	8863	14491	7590
15	11014	15227	16523	16743	20995	14513	14158	11038	15150	16951	15676	11199*	8609	6887	6904	17180	11521	11933

Table 7. Individual food biomass (g) consumed by cod (ages 3-15) during their residence in Area 4T (May-November). Values indicated with an asterick are averages for the corresponding ages.

	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	79	80	81
3	696	658	583	1199	715	752	771	715	846	808	827	808	808	752	640	489	677	1032
4	2040	2004	2066	1574	1591	1242	1668	1200	2045	1039	1793	1458	1518	1591	1393	1417	1509	1501
5	1872	1766	1533	1284	1298	1357	1517	2149	3124	1680	2929	1429	2088	1316	2384	1925	1848	1274
6	2266	2627	2149	1786	1457	1597	1695	1990	2496	1950	3113	1698	2193	1948	2238	2603	1916	1746
7	2717	3445	2615	2505	1689	1993	2283	2521	5362	3480	4803	3091	3247	1910	2615	2836	1989	2204
8	3633	4584	3769	3291	2662	2797	2659	3210	1612	3517	3511*	3511*	5228	2745	3513	2927	4695	5346
9	4748	7062	8137	3920	5014	3735	3848	4062	4525	5898	4018	4903*	3586	6460	3522	5086	5701	4030
10	4901	6602	7929	4908	6717	5490	4782	5088	6872	7118	4201	5851*	3512	6680	5193	8064	6551	4859
11	5891	8705	9100	6653	6967	7789	6751	6919	5403	7236	5460	6902*	6883	8087	5504	4632	7469	7890
12	7402	8863	9415	5585	10200	7534	8136	7809	8233	8148	5903	7769*	8663	6660	8721	6354	7896	6556
13	10957	11285	12491	8382	7327	10867	10615	9590	9412	11038	7321	9011*	3478	8041	4759	6715	11074	9844
14	11757	8665	12637	11888	12945	8440	14882	11578	11242	11295	4018	9778*	7201	7995	7008	7148	11619	5908
15	8582	12508	13769	12749	16603	11230	11090	8790	12035	14054	11961	10756*	6316	5749	5383	13571	9307	9156

Table 8. Total food biomass (September) consumed by cod age-groups 3-15 in a defined area in the southwestern Gulf of St. Lawrence. Values are given in tons.

	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	79	80	81
3	3911	3479	1052	2818	1158	1788	1574	1696	3487	2992	1827	1622	2328	906	1057	300	7084	3211
4	7076	9029	8797	2268	2989	1615	3046	1810	3601	3310	5237	2521	2415	3249	1201	7894	7646	12748
5	4658	4559	5080	4096	1367	1834	1382	2484	3090	1909	6401	2812	2491	1315	2749	6259	7697	4872
6	2657	4189	3747	4329	3000	1043	1313	1069	1650	1186	2212	2208	2525	1334	1097	6021	4005	4996
7	1257	2209	2356	2718	2735	2261	754	1012	1572	1379	1733	1310	2345	1128	875	1229	2965	2959
8	977	934	1300	1642	1614	2410	1393	494	373	562	791	732	1133	1007	930	625	1210	5117
9	1701	687	974	797	1311	1126	1620	975	391	840	354	563	394	663	580	538	720	667
10	728	908	432	349	797	744	676	1069	928	382	360	229	202	350	228	483	410	394
11	467	356	598	217	273	565	459	450	646	522	174	300	117	217	122	58	281	317
12	372	261	165	209	214	166	355	243	248	540	223	104	133	55	103	49	46	159
13	207	238	186	63	185	135	128	220	146	132	263	185	16	32	15	19	50	37
14	165	58	150	102	61	143	108	65	145	73	18	208	75	19	7	33	16	17
15	78	66	45	78	90	30	104	36	34	108	32	23	74	30	5	26	29	8
3-15	24253	26974	24880	19686	15794	13860	12913	11625	16309	13936	19624	12817	14248	10305	8967	23535	32158	35501

Table 9. Biomass of herring (tons) consumed by cod age-groups 3-15 in a defined area in the southwestern Gulf of St. Lawrence in September of each year indicated.

	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	79	80	81
3	49	48	0	80	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	429	177	92	91	0	0	0	0	0	0	0	0	0	0	13	0	0	0
5	448	189	0	168	0	0	0	0	91	0	74	0	0	0	36	0	0	0
6	308	409	410	216	0	0	24	0	16	27	90	103	28	0	23	0	0	0
7	190	847	613	306	0	176	0	0	0	62	325	228	156	0	16	0	79	7
8	268	282	115	473	150	103	32	19	0	63	155	308	252	76	31	0	34	0
9	465	142	209	265	349	447	462	383	16	261	166	237	152	243	92	0	79	0
10	199	187	93	116	212	295	193	420	37	119	169	96	78	128	36	0	45	0
11	179	0	0	3	0	151	122	260	378	272	108	161	12	29	34	9	0	0
12	143	0	0	3	0	44	94	140	145	281	139	55	14	7	29	8	0	0
13	79	0	0	1	0	36	34	127	85	69	163	99	2	4	4	3	0	0
14	63	0	0	1	0	38	29	37	85	38	11	111	8	2	2	5	0	0
15	30	0	0	1	0	8	28	21	20	56	20	12	8	4	2	4	0	0
3-15	2850	2280	1532	1724	711	1298	1017	1408	873	1247	1419	1410	709	494	318	29	238	7

Table 10. The ratio (x100) of herring biomass consumed to total food biomass consumed by cod age groups 3-15 in a defined area and for a given period (September) in each year indicated.

59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	79	80	81
11.7	8.5	6.2	8.8	4.5	9.4	7.9	12.1	5.4	8.9	7.2	11.0	5.0	4.8	3.5	0.1	0.7	0.0

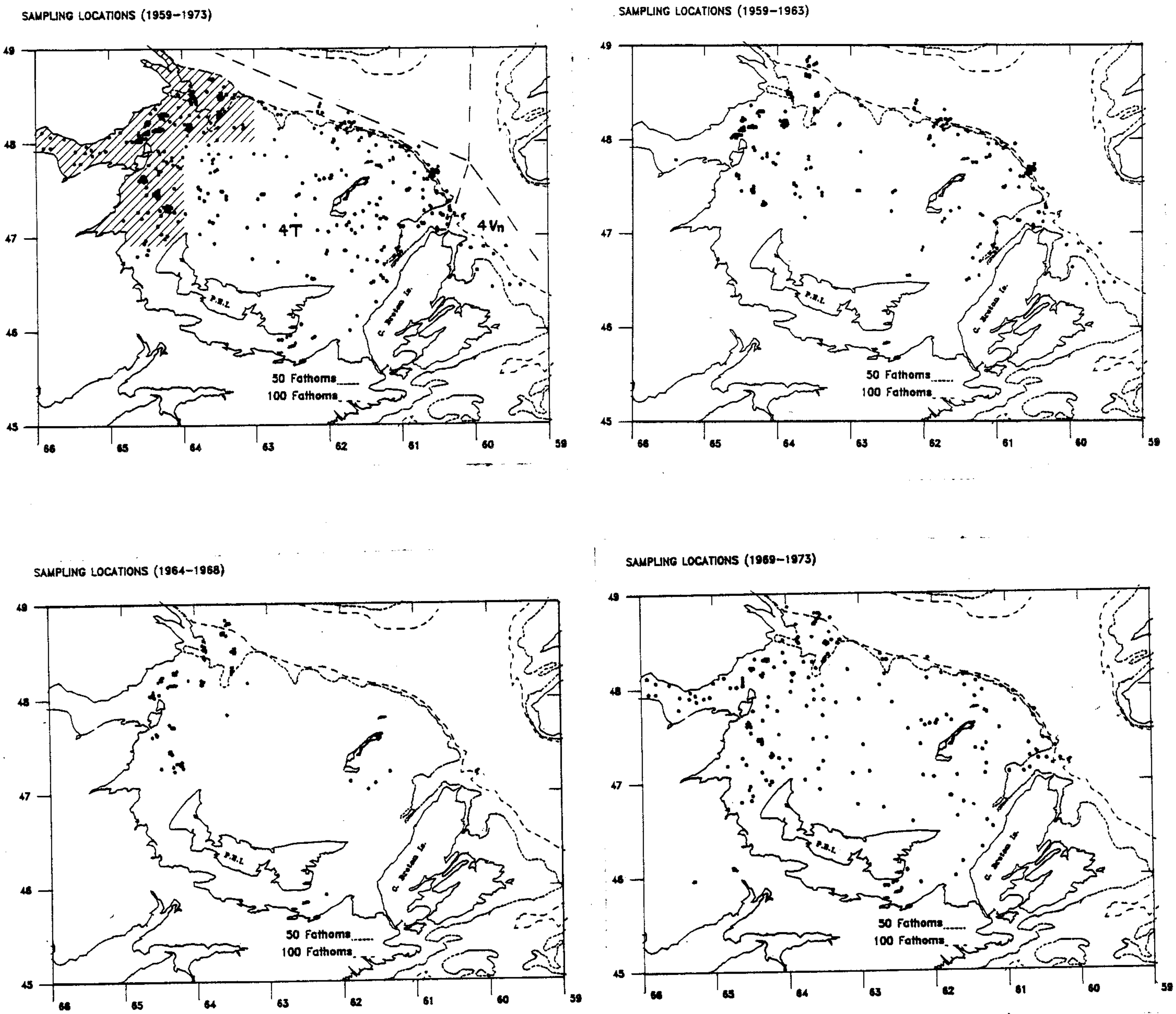

Fig. 1. Sampling locations for cod stomach content analysis in 1959-73, 1959-63, 1964-68, and 1969-73. Analysis was conducted on research cruises at various time of the year. The cross-hatched area is that referred to in the yearly analysis of cod diet (see text).

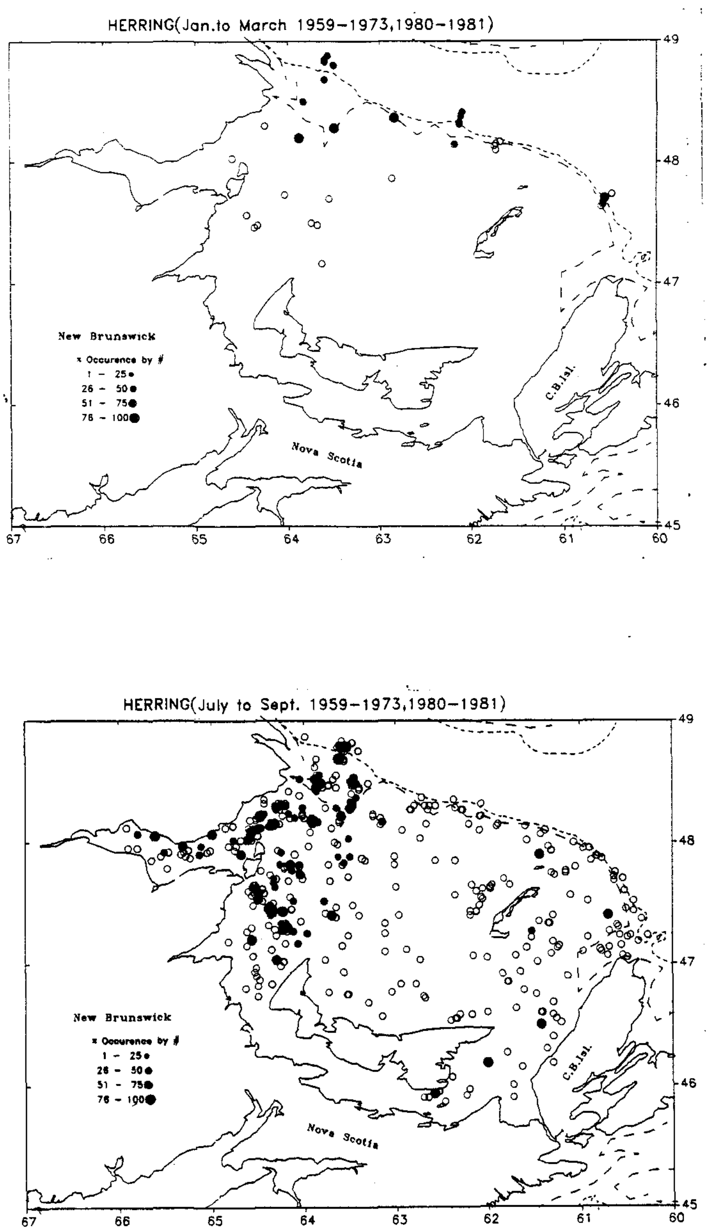

Fig. 2. Geographic distribution (by season) of herring predation by cod. Data were collected from groundfish surveys in the southern Gulf of St. Lawrence (1959-73 and 1980-81)

$$\% \text{ occurrence} = \frac{\text{no. of cod containing specific prey}}{\text{no. of cod in sample}} \times 100$$

Open circles denote sets with 0% occurrence.

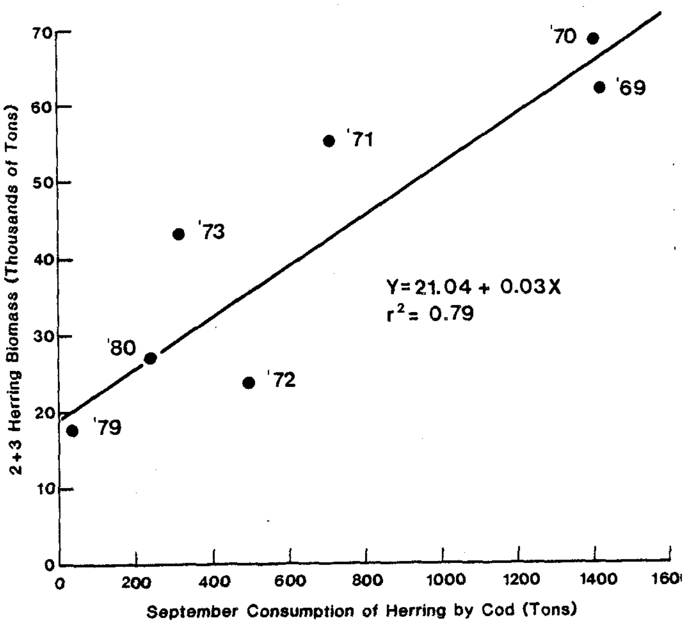

Fig. 3. Relation between 2+3 herring biomass (from Cleary 1981) and the September consumption of herring by cod in a defined area in the Gulf.

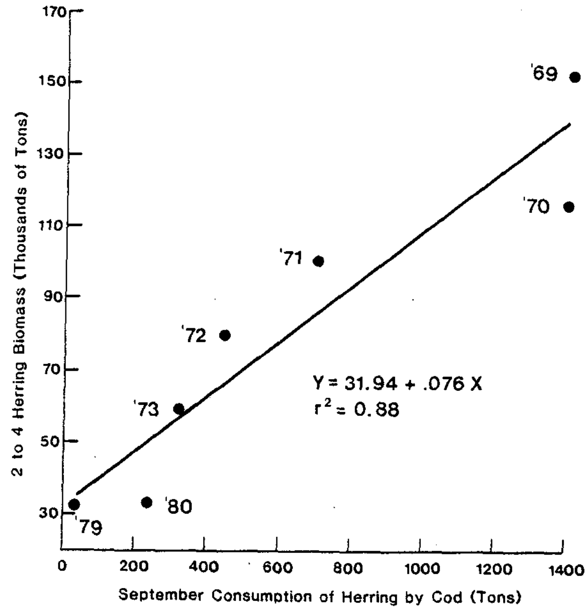

Fig. 4. Relation between 2 to 4 herring biomass (from Cleary 1981) and the September consumption of herring by cod in a defined area in the Gulf.

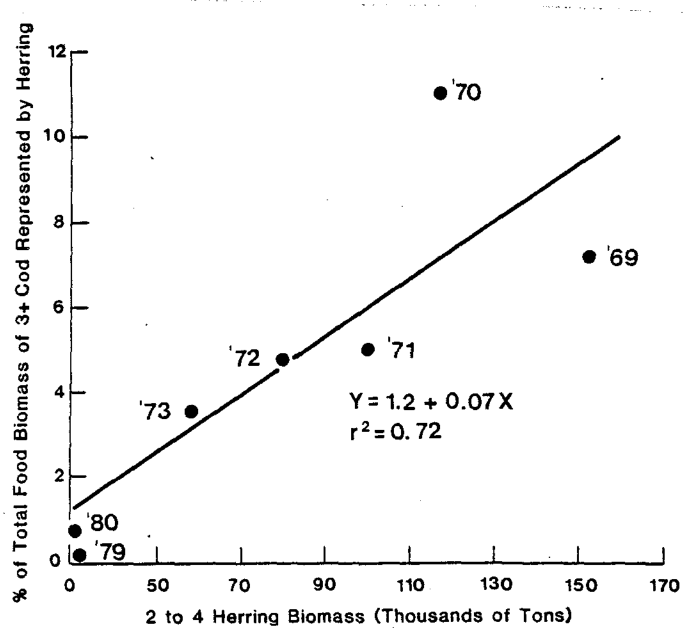

Fig. 5. Relation between 2 to 4 herring biomass (from Cleary 1981) and the ratio of herring food biomass to total food biomass (x100).