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Recent changes in the feeding of cod (*Gadus morhua*) off the Flemish Cap, Newfoundland 1989–1993

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The food and feeding of Flemish Cap cod are described for 5 years based on 3921 stomachs collected in the fishing grounds off the Flemish Cap, Newfoundland in summer 1989–1993. Feeding intensity was high but the prey spectrum was narrow in all years with hyperiids and redfish (*Sebastes* sp.) predominating. Squid and polychaetes had a high inter-annual variability. Juvenile cod diet was dominated by crustaceans, mainly hyperiids, and polychaetes, while in adult cod diet the most important prey were fish, mainly redfish. The maximum size of redfish eaten increased with cod size, but prey–predator size relationships showed weak correlation. Cannibalism increased in 1991 (mainly upon 1-year-olds), coinciding with the appearance of a large year class in 1990. In the years 1992 and 1993, a change in the diet was observed involving an increase of hyperiids in the adult cod diet and a decline of redfish.

Key words: Atlantic cod, *Gadus morhua*, feeding, redfish, Flemish Cap.

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Introduction

In recent years, a decrease in biomass has been observed for several commercial species, including cod, in the north-west Atlantic. The trends from 1989 to 1991 are particularly dramatic and suggest not only a decline, but a concentration of the remaining biomass in the offshore areas (Atkinson, 1993). Changes were also observed recently in the Flemish Cap, with the adult biomass of cod and plaice decreasing (Sinclair, 1994) and an accompanying marked increase in shrimp biomass which has resulted in a new fishery in this area (Parsons, 1994).

This study is aimed at determining possible changes in the food and feeding patterns of cod off the Flemish Cap in recent years. Although sampling was limited to the summer period, the qualitative composition of the cod diet in this area is not very different during the rest of the year (Albikovskaya and Gerasimova, 1993). The months studied, however, correspond to the period of highest feeding intensity (Turuk, 1981).

Materials and methods

Stratified-random bottom trawl surveys were carried out by the European Economic Community on Flemish Cap NAFO, Div. 3M, between 46°10′–48°30′N and 43°50′–46°40′W from 1989 to 1993. Although the research vessel used was not the same in all years, the survey procedure followed was identical and standardized.

The vessels were large stern trawlers fishing with a bottom otter trawl lined with 35 mm mesh in the codend. Tows were for 30 min at 3.5 knots, and the daily period for fishing was from 06.00 to 22.00 h. Further descriptions of the area sampled and sampling procedures were given by Vázquez (1990, 1995). Some results for 1993 data (R. Marín *et al.*, 1994) are included in this study.

Total lengths of cod were measured immediately after capture to the nearest cm and each individual was weighed to ±5 g. Otoliths were extracted, stored and used to age the cod later in the laboratory.

Stomachs were dissected out on a board by cutting the oesophagus and the intestine behind the pyloric sphincter and were then frozen. Stomachs with evidence of regurgitation were not used. Stomach contents were examined in the laboratory and the food components were separated and identified to the lowest possible taxonomic level. Food items in each taxon were placed briefly on absorbent paper to remove excess liquid, and then weighed to ±0.01 g. The number of

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Table 1. Stomach samples of cod taken between 1989–1993 on the Flemish Cap, NAFO Div.3M.

Year	Sampling dates	Sampling platform	Number of hauls	Depth range (m)	Stomach numbers analysed by age								Total	Feeding intensity (%)
					1	2	3	4	5	6	7	>8		
1989	6 July–12 August	"Cryos"	58	144–459	7	7	242	467	387	55	9	8	1182	92.6
1990	12 July–8 August	"Ignat Pavlyuchenkov"	64	128–428	30	85	44	106	103	86	28	34	530	95.5
1991	14 June–17 July	"Cornide de Saavedra"	44	144–406	52	38	70	16	111	67	18	8	380	90.8
1992	23 June–24 July	"Cornide de Saavedra"	54	128–640	147	269	91	88	22	113	23	2	755	87.4
1993*	15 June–18 July	"Cornide de Saavedra"											960	96.0

*R. Marín *et al.*, 1994.

stomachs collected by age group and year is presented in Table 1.

The feeding intensity index (FI) of cod by each year was calculated as:

$$\mathrm{FI}=\frac{SN_f}{SN_t}\times 100$$

where SN_f is the number of stomachs with some food and SN_t is the total number of stomachs analysed. The relative importance of individual prey items was assessed using indices of frequency of occurrence and weight (Amézaga, 1988).

The prey occurrence index (OI): The number of stomachs in which a prey item occurred was expressed as a percentage of the total number of stomachs investigated.

The gravimetric index (GI): The weight of each prey item in all stomachs in the sample was expressed as a percentage of the weight of the total stomach contents in the sample. Other indices calculated were as follows. The Simpson feeding diversity index (D) is obtained from

$$\mathrm{D}=1-\sum_{i=1}^{s}\frac{N_i(N_i-1)}{N(N-1)}$$

where N_i is the number of times in which the type of prey appears in the total number of stomachs, N is the number of times in which all prey appear in the total number of stomachs, and s is the number of types of prey.

The diet overlap index is obtained from the Schoener diet overlap index (R_0) (Linton *et al.*, 1981), given as:

$$R_0=1-\frac{1}{2}\sum_{i=1}^{n}|P_{ij}-P_{ik}|$$

where P_{ij} is the frequency of appearance of prey i in individuals of class j, P_{ik} is the frequency of appearance of prey i in individuals of class k and n is the number of length classes.

The diet overlap was calculated intra-specifically (Wallace and Ramsey, 1983) for the three cod groups: pre-recruits (<3 years old with lengths <35 cm); recruit juveniles (3–5 years old with lengths between 35 and 56 cm) and adults (>5 years old with lengths >56 cm). Following Mathur (1977), diets were considered to overlap for values of $R_0>0.6$.

The number of stomachs collected showed a non-normal distribution by length groups. For this reason we used the Kruskal–Wallis test to test the null hypothesis that the stomach contents of cod on the Flemish Cap in summer were not different in the years 1989–1992. The analysis was based on the gravimetric index for the most important prey (GI>2%) and processed with the standard statistical program 3S (BMDP) (Dixon *et al.*, 1990).

To avoid the variability of the wide cod size range, as well as their different distributions in the years studied, the analysis was used with 10 cm length groups. Furthermore, a multiple comparison test by year-pairs was carried out. For this test, the *Z* statistic is computed for a variation of the Mann–Whitney test (Hollander and Wolfe, 1973). In this test, the null hypothesis is rejected if "ZSTAT" is larger than the critical value "ZC", where $1-\mathrm{PHI(ZC)}=\mathrm{ALPHA}/(\mathrm{K}(\mathrm{K}-1))$, PHI is the cumulative standard normal distribution function and K is the number of groups compared. With four groups, the critical value is: 2.64 for overall ALPHA of 0.05 and 2.39 for overall ALPHA of 0.10.

A linear regression and the correlation parameters for predator length (cod) and prey length (redfish) were calculated for each year.

When it was not possible to measure the total length of redfish ingested, the lower jaw bones were measured to the nearest mm with a calliper and the relationship of mandible length/total length from Paz *et al.* (1993) was used to estimate the total length of redfish.

Results and discussion

The summer feeding intensity (Table 1) was higher than 85% in all years. This high value coincides with the seasonal feeding pattern (Albikovskaya and Gerasimova, 1993). The number of prey species of cod was small and coincided with the narrow prey spectrum off the Flemish Cap (Konstantinov *et al.*, 1985).

Table 2. The diversity index by cod length class (cm) in Div. 3M 1989–1992.

Year	<20	21–30	31–40	41–50	51–60	61–70	71–80	Mean ± S.D.
1989	—	0.50	0.33	0.43	0.68	0.59	0.75	0.55 ± 0.16
1990	0.59	0.60	0.58	0.53	0.61	0.77	0.58	0.61 ± 0.80
1991	0.46	0.56	0.54	0.75	0.74	0.78	0.85	0.70 ± 0.13
1992	0.35	0.35	0.48	0.57	0.62	0.62	0.72	0.56 ± 0.13

Table 3. Gravimetric index (%) and occurrence index (%) of food items of cod (lengths combined) in Div-3M. July 1989–1993.

	1989		1990		1991		1992		1993
Food items	GI	OI	GI	OI	GI	OI	GI	OI	OI
O. Actinida	*	0.27							
Class Ctenophora	0.1	0.18							
Class Polychaeta	0.4	0.64	0.9	8.30	1.7	6.38	0.4	2.26	6.1
Phylum Echinodermata	0.1	0.55	*	0.59	*	2.31			
Class Cephalopoda	0.7	1.55	1.5	5.14	2.7	8.11	0.6	2.26	1.6
Other mollusca	0.2	0.27	0.1	0.79	*	0.29			
O. Copepoda	0.2	1.73	0.2	2.57	0.9	1.16	1.5	6.25	
Fam. Hyperiidae	59.1	66.82	65.4	75.49	56.3	70.14	84.4	91.49	84.2
Shrimp**	3.7	12.16	6.9	26.38	6.6	33.04	2.7	14.76	6.5
Other crustacea	0.5	1.46	0.7	4.55	1.3	7.83	0.5	2.26	
Sebastes sp.	17.5	19.10	17.5	19.57	20.6	30.72	3.3	7.31	5.6
Gadus morhua	0.2	0.27	1.8	2.96	4.0	6.08	2.4	3.19	
Anarhichas sp.	0.7	1.55	0.2	0.79	1.9	1.16	0.2	0.66	
Family Myctophidae	0.1	0.64	*	0.79	1.0	0.29	*	1.46	
Family Cottidae	*	0.09	0.1	0.20			1.3	2.22	
Family Macrouridae	*	0.18	*	0.20					
Other pisces	0.6	1.00	0.4	0.99	1.4	1.74	0.9	1.73	4.4
Unidentified pisces	9.6	6.21	3.0	7.91	3.5	10.43	1.3	5.59	
Unidentified	5.9		1.0		0.6		0.2	0.80	
No. Stomachs	1094		506		345		752		911
% empty stomachs	7.44		4.5		9.2		13.5		3.8

*Traces.
**Mainly *Pandalus borealis*.

Crustacean prey items, especially hyperiids, gammariids, and shrimps (mainly *Pandalus borealis*), some small cephalopods (mainly *Semirrosia* sp.), ophiuroids and polychaetes were present in almost all length ranges sampled, other cephalopods (*Illes illecebrosus*, *Onychoteuthis banksii*), decapods (*Lithodes maja*) and echinoderms (except ophiuroids) only appearing in adult specimens. Juvenile redfish were the dominant fish prey in all length ranges. The other fish (*Gadus morhua*, *Serrivomer beani*, *Anarhichas* sp., *Lumpenus lumpretaeformis*, *Triglops murrayi*, myctophids) had a low occurrence and a different distribution in the cod length groups studied.

The feeding diversity in the period studied is shown in Table 2. The mean index increased with cod length. In the years 1990 and 1991 the mean value of feeding diversity was larger than in other years, probably due to the high frequency of shrimps and polychaetes in the diet of juvenile cod and of squids in adult cod (Table 3, Fig. 1).

Occurrence index (OI) and gravimetric index (GI) show the prevalence of hyperiids in the cod diet in all years (Table 3, Fig. 2). The value of the GI and OI for the hyperiids was greater than 56% and 66% respectively.

As shown in Figure 1, the gravimetric index of the hyperiids decreased with increasing cod size. The atypical value for the small cod (<20 cm) in 1989, was possibly due to the limited sampling for that length range. Fish (mainly redfish) eaten increased in length with cod length in all years. This feeding pattern by length remained similar throughout the period studied.

Fish were incorporated into the diet at cod lengths greater than 21 cm, and in all years their presence increased with increasing cod size. Redfish was the most

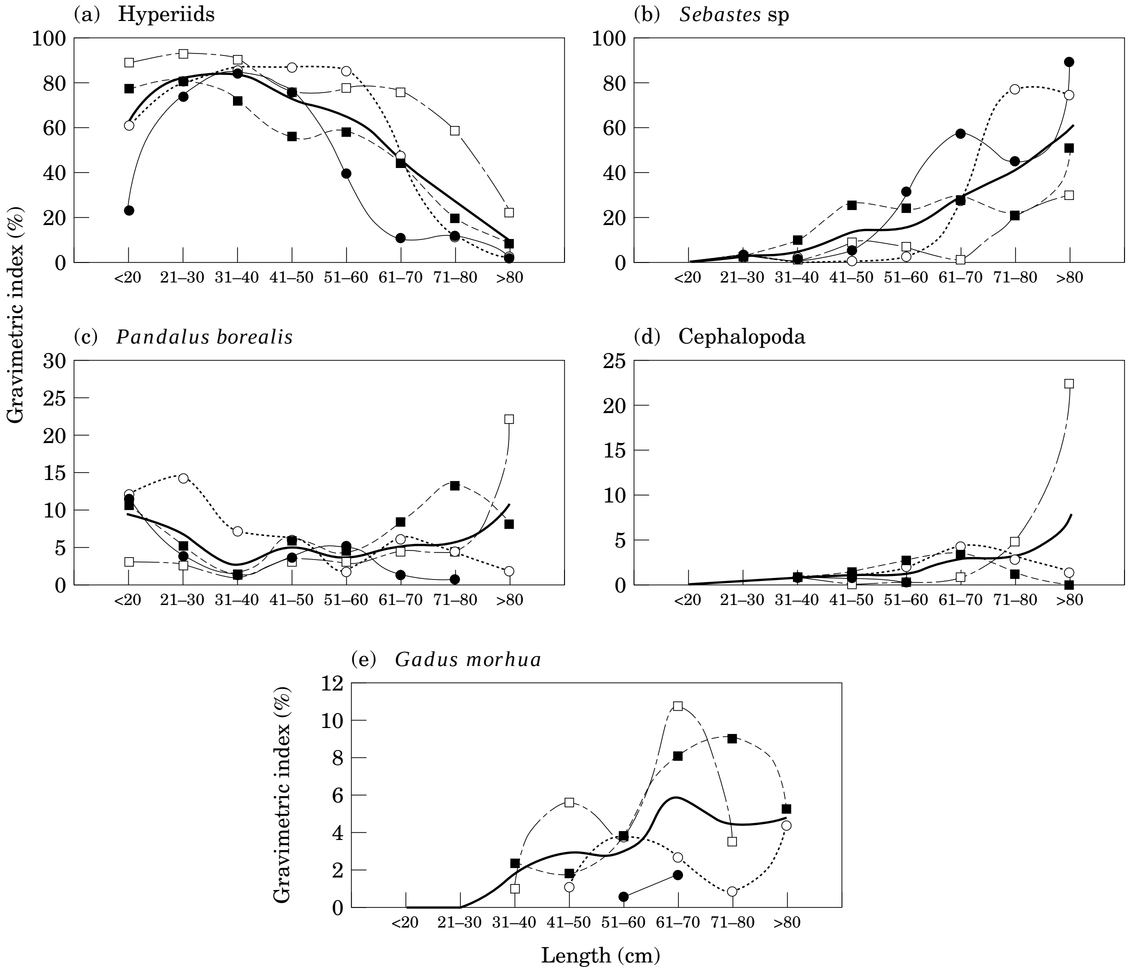

Figure 1. Gravimetric index by cod length groups in the period 1989–1992 for (a) hyperiids, (b) redfish, (c) shrimp, (d) cephalopods and (e) cod. ●=1989; ○=1990; ■=1991; □=1992. The bold line represents the mean.

important fish prey (Table 3, Fig. 2). It is interesting to note that 0-group cod caught in a few pelagic trawls in 1990 had preyed on redfish larvae, although age group 1 did not prey on redfish and age group 2 had very low predation rates on fish.

The gravimetric index and relative frequency of occurrence for the main prey groups by year are also shown in Figure 2. The years 1992 and 1993 show an important increase in the number of hyperiids taken and the decreasing importance of redfish (Fig. 2(b)). The gravimetric index values, only available until 1992, also confirm this pattern (Fig. 2(a)).

The increase of the gravimetric and occurrence index values of squids (mainly *Illex illecebrosus*) in 1990 and 1991 (Table 3) correspond with the greater catch rates of squids in the surveys of these years (Vázquez, 1991, 1992) also indicating that Atlantic cod is an opportunistic feeder on the most abundant and available prey species.

From the Kruskall–Wallis test performed by 10 cm length groups to compare the similarity or differences in the cod summer diet during the years 1989–1992, we observed that hyperiids, redfish and shrimp showed significant differences in all length ranges considered. The cephalopods and cod (the least important prey of five studied) had no significant differences in some length ranges.

In relation to the multiple comparison test by year pairs carried out from the modified Mann–Whitney test, we point out the following results:

(a) For the hyperiids GI values in the adult cod diet (mainly at 61–80 cm cod length) for the years 1989 and 1992 differ significantly ($Z>2.64$) from 1990 and 1991. This coincides with the low values of GI in 1989, and high values in 1992 (Fig. 1(a)) and confirms the substantial increase of hyperiids in the adult cod diet in the later years.

(b) The redfish GI corresponding to juvenile cod at 1991 (<50 cm) was significantly different ($Z>2.39$) from

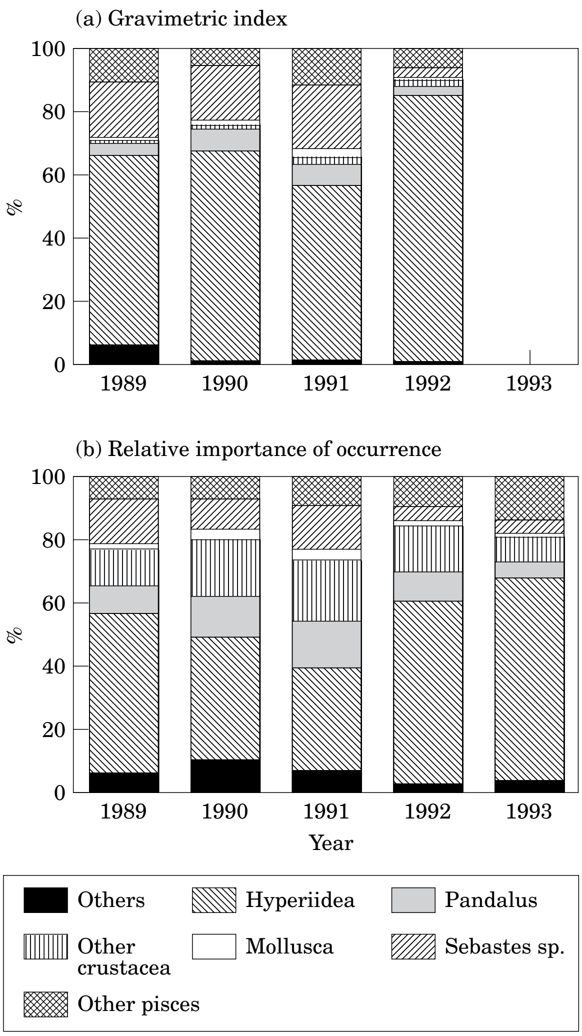

Figure 2. Food composition for the main prey groups of Flemish Cap cod expressed as (a) gravimetric index and (b) relative importance of occurrence (summing the individual importance values, and calculating the percentage each makes of the total) in Summer 1989–1993. The category other crustacea contained mainly decapods.

other years. The importance of redfish in this size range was higher, possibly due to a greater presence and abundance of the small juvenile redfish (7–8 cm) in the area.

(c) For the *Pandalus borealis* GI value, 1990 and 1991 were significantly different from 1989 and 1992 in cod length ranges of 21–40 cm and 51–70 cm respectively. In 1990 and 1991, the presence of a strong year class of *Pandalus borealis* contributed to the biomass increase in the area (Sainza, 1994). This fact could be the reason for the high values of the gravimetric index in size range 21–40 cm in 1990 and in the larger sizes (51–70 cm) in 1991.

Table 4. The overlap index of Schoener in Div. 3M, in summer 1989–1992 for three groups of cod: group A (<35 cm), group B (35–56 cm), group C (>56).

	1989	1990	1991	1992
(A–B)	0.8	0.9	0.7	0.8
(B–C)	0.5	0.4	0.5	0.8
(A–C)	0.3	0.4	0.3	0.7

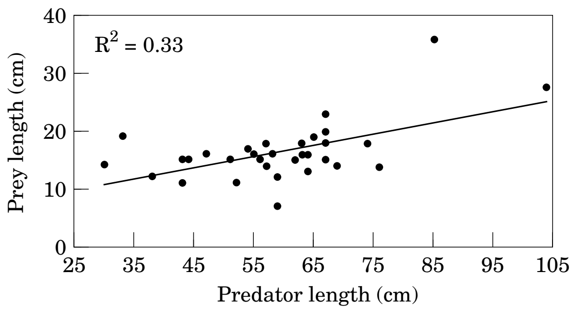

Figure 3. Plot of prey size vs. predator size for Flemish Cap cod: 1989–1992. Correlation given as R^2 values.

The diet overlap calculated intra-specifically provides a better idea of the feeding similarities between the three length groups considered. The results obtained for the years 1989–1992 are shown in Table 4.

Following the Mathur overlap criterion (Mathur, 1977), we can see that the cod diet changes between groups B and C in 1989, 1990 and 1991. This indicates the similar trophic habits (mainly small crustaceans) of the pre-recruits and immature recruits in these years. The diet change was mostly due to incipient predation on small redfish.

For 1992, there was overlap between all groups. The overlap index between groups A and C increased in this year, compared with earlier years. The overlap in the diet between all length groups corresponds with the decrease of redfish predation and increase of hyperiids in the adult cod diet.

During the period studied cannibalism was present in 63 cases, of which the predated cod could be measured 34 times. The length range of predators was wide, 30–104 cm, and the prey length range was from 11 to 36 cm. The relationship between predator and prey length was significant ($n=32$, $p<0.001$), although a determination coefficient (R^2) of 0.33 was obtained for the linear regression function (Fig. 3). Flemish Cap cod can consume cod prey up to about 57% of their own length, but most prey were much smaller, 10–20 cm, corresponding to one-year-old length (Fig. 4).

The cannibalism rate increases, in general, with predator size (Fig. 1(d)), and so its value will bear a relationship to the length distribution of the sample.

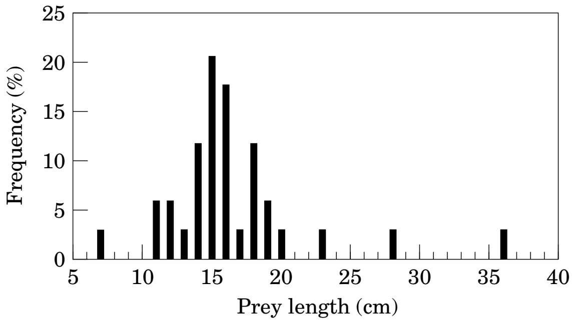

Figure 4. Numerical distribution (%) of Flemish Cap cod as prey of cod with respect to prey length. Summer 1989–1992 (n=34).

Table 5. Correlation coefficients between predator and prey length.

Year	n	r	p	Regressions
1989	136	0.69	<0.001	y=0.426+0.239x
1990	58	0.52	<0.001	y=4.865+0.205x
1991	84	0.62	<0.001	y=0.668+0.171x
1992	44	0.56	<0.001	y=1.693+1.467x
1989–92	322	0.62	<0.001	y=0.224+0.223x

This could make it difficult to compare the years sampled. However, the annual differences in the cannibalism rate, expressed as OI and GI (Table 3), were not affected for this reason.

The incidence of cannibalism increased in 1991 (mainly in 1-year-olds) and coincided with the appearance of a large year class in 1990 which was the largest of those observed in the period 1988–1994 (Vázquez, 1995b). Lilly (1987) reported a similar phenomenon in 1982 when the cannibalism increase coincided with the appearance of an abundant year class in 1981.

Although the number of juvenile cod eaten by conspecific predators may be influenced by several factors (Bogstad *et al.*, 1993), from our results, the importance of cannibalism was related to the abundance of the 1-year-old year class.

Predation on redfish

The dominant prey of adult cod on the Flemish Cap in summer is small redfish. Although the abundance of small juvenile redfish (up to 20–22 cm) was higher in 1992 than in preceding years (Vázquez, 1993), the occurrence of this prey in the cod stomachs was less. In the years 1992 and 1993, hyperiids were the main prey in cod diet for all size groups (Fig. 1).

The correlation coefficient between predator length (cod) and prey length (redfish) was calculated for each

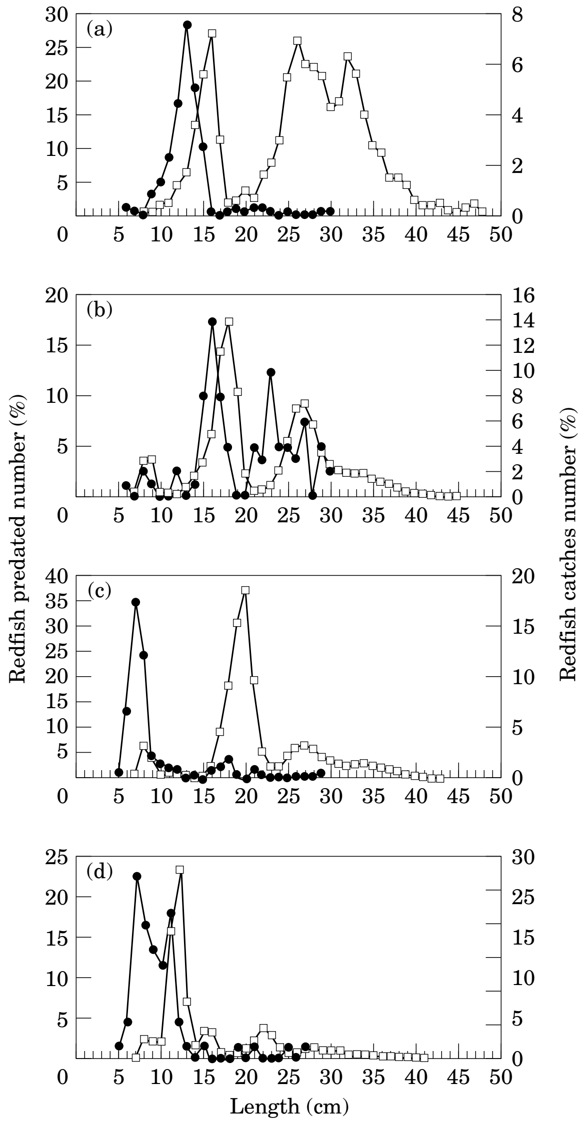

Figure 5. Comparison of small juvenile redfish abundance from trawl data with redfish recovery in the stomach contents of cod for NAFO Div. 3M: (a) 1989, (b) 1990, (c) 1991 and (d) 1992 (● predated, □ caught).

year (Table 5). These values indicate a weak relationship. The accessibility of the small juvenile redfish in terms of abundance and presence in the area is more important than their size.

The abundance of redfish by length-class in the trawl catches and the number of redfish by length-class recovery in the stomach contents, shown in Figure 5, were compared as a percentage of the total redfish caught and predated. The most abundant small juvenile redfish (<20 cm) were those most preyed upon. In the years 1989 and 1990, however, there are differences between redfish predated and redfish modal lengths estimated from trawl catches. This modal length gap was 13–16 cm in 1989 and 16–18 cm in 1990.

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