ICES Journal of Marine Science (2011), 68(9), 1909–1917. doi:10.1093/icesjms/fsr104

Food and feeding habits of cod (*Gadus morhua*) on the Faroe Bank

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Magnussen, E. 2011. Food and feeding habits of cod (*Gadus morhua*) on the Faroe Bank. – ICES Journal of Marine Science, 68: 1909–1917.

Received 16 July 2009; accepted 6 May 2011; advance access publication 23 June 2011.

Data from ten bottom surveys on the Faroe Bank during the years 1994–1998 are used to describe the feeding habits of cod on the Faroe Bank. Cod are clearly omnivorous in their diet. Overall, fish were found in 82% of the stomachs, accounting for 59% of the food by weight, but just 35% of the food items by number. Of the fish, lesser sandeel was the most common, making up 78% of the fish biomass consumed. Cannibalism was practically non-existent. In some years, the squid *Loligo forbesi* formed an important component of the diet, was the main food and identified in up to 64% of the stomachs, and constituting 60% by weight of the diet; in other years, it was a negligible part. Crustaceans were found in 48% of the stomachs, accounting for 16% by weight but as much as 44% by numbers. The diet of cod shifts ontogenetically, with stomach fullness greater and nutrient quality of prey higher for cod <70 cm.

Keywords: cod, condition factor, diet, Faroe Bank, *Gadus morhua*, stomach contents, stomach fullness index (SFI), temporal variation.

Introduction

The growth rate of cod (*Gadus morhua*) on the Faroe Bank is considered to be one of the fastest in the world (Magnussen, 2007). On average, a 3-year-old cod from the Faroe Bank is ~73 cm long and weighs ~4.9 kg, whereas a cod of the same age on the nearby Faroe Plateau is, on average, just 55 cm and 1.7 kg (Magnussen, 2007), ~45 cm long in Iceland (Taylor, 1958), 61 cm in the North Sea (Jennings *et al.*, 1999), 37 cm in the Barents Sea (Taylor, 1958), and just 21 cm in Newfoundland (NAFO subarea 2J; May *et al.*, 1965).

The fast growth is especially pronounced during the first 3 years of life; it then slows down and is comparable with that of cod on the Faroe Plateau (Faroe Marine Research Institute, unpublished data). The early growth of a fish can be expressed for comparative purposes by the time it takes to attain half its asymptotic length ($t_{0.5L_\infty}$). Rearranging the von Bertalanffy growth equation, $t_{0.5L_\infty} = (\ln 2/K) + t_0$, where L_∞ is the asymptotic length, K the rate of growth towards the asymptotic value, and t_0 the time at which length is zero in the modelled growth trajectory. Using the von Bertalanffy growth parameters presented by Magnussen (2007), young Faroe Bank cod grew fastest of 18 cod populations in the North Atlantic and attained half their asymptotic length (L_∞= 122 cm) after just 2.3 years. For the Faroe Plateau and North Sea cod, half the asymptotic length is attained in 3.2 years, for Newfoundland cod (NAFO area 3L) 5.5 years, for Iceland cod 5.7 years, and for North Norwegian cod as much as 10 years.

The Faroe Bank is located ~75 km southwest of the Faroe Islands at ~60°55′N 08°40′W (Figure 1). It is separated from the Faroe Plateau by the deep, narrow Faroe Bank Channel. Hydrographic investigations have demonstrated an anticyclonic current on the bank (Hansen *et al.*, 1999), and these topo- and hydrographic properties have led to a fairly isolated ecosystem there, which has caused various types of specialization of morphological and physiological nature, and different genetic properties of some of its fish from the same species elsewhere (Schmidt, 1930; Love *et al.*, 1974; Mattiangeli *et al.*, 2000, 2002). For cod, tagging experiments have demonstrated that Faroe Bank cod are isolated from the nearby Faroe Plateau cod and other cod populations (Strubberg, 1916, 1933; Tåning, 1940; Joensen, 1956; Jones, 1966), the separation having led to distinctive genetic properties that distinguish Faroe Bank cod from other cod populations (Dahle, 1995; Joensen *et al.*, 2000; Nielsen *et al.*, 2009).

The fast growth rate reported for Faroe Bank cod has been demonstrated too for other cohabiting fish species. In an interpopulation comparison of the growth patterns of 14 common fish species on the Faroe Bank, Magnussen (2007) found that stocks resident on the Faroe Bank grew faster and were, on average, 36% larger when they reached sexual maturity than contemporary stocks of the same species elsewhere. Cod were, on average, 106% larger than the cod from 17 other North Atlantic cod populations compared. The fast individual growth rate for Faroe Bank fish was ascribed mainly to the favourable temperature and the abundance of food. However, no rigorous investigation has been carried out to confirm this qualified assertion. Rae (1967), du Buit (1982), and Nicolajsen (1993) provided general descriptions of cod feeding habits on Faroese grounds, but did not have the Faroe Bank as a separate area in their work. Steingrund (2009) did compare the feeding conditions and depth distribution of cod on the Faroe Plateau and Faroe Bank, but in general, provided limited diet information for the Faroe Bank stock. Indeed, biochemical investigations of Faroe Bank cod showed high liver glycogen and low water content in the flesh (Love *et al.*, 1974), indicating large reserves of energy and good feeding conditions. It was therefore deemed to be of value to model food energy intake in relation to food consumption and temperature (e.g. Wootton, 1990; Krohn

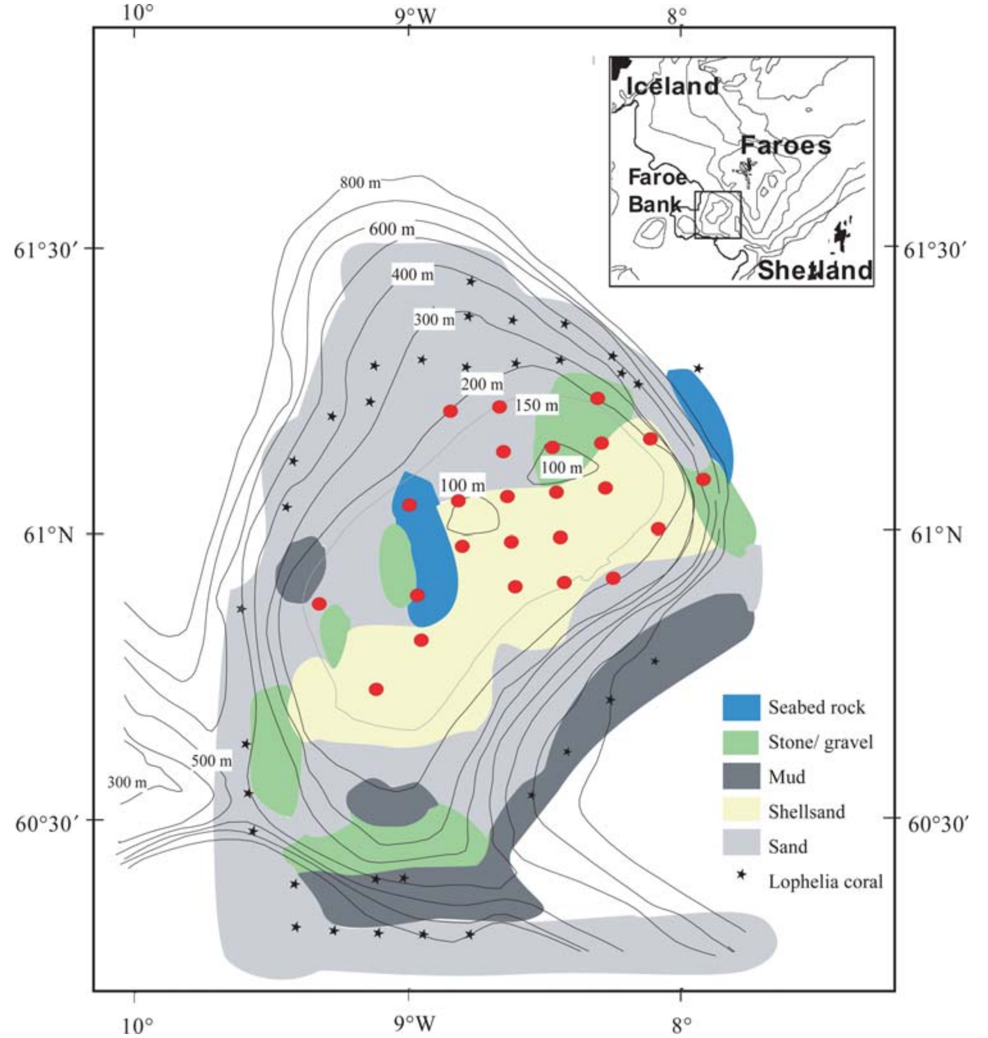

Figure 1. Geographic location and seabed characteristics of the Faroe Bank. The red dots are the selected stations (modified from Magnussen, 2002).

et al., 1997). Before that can be done, though, the feeding habits of the fish species need to be known.

The purpose of this paper is to give a general description of the feeding habits of cod on the Faroe Bank. The types and quantities of different prey species are listed, and information on how these vary in time, seasonally as well as annually, is given.

Material and methods

Cod were collected on the annual spring and autumn surveys performed on the Faroe Bank by the RV "Magnus Heinason". In all, 1077 cod stomachs were collected during the ten surveys performed on the Faroe Bank from 1992 to 1998 (Table 1). To start, surveys were only carried out in spring, but in 1996, the programme was extended so that the diet could be investigated during autumn too. Demersal surveys of the Faroe Bank were designed mainly to study cod, haddock (*Melanogrammus aeglefinus*), and saithe (*Pollachius virens*), and the same stations were occupied each year, deploying the same type of trawl: a 116-foot (35.4 m), 4-panel bottom trawl with 18 m between the wings of the groundgear and 40 mm nominal mesh size in the codend. Tows were of 60 min duration at a speed of ~3 knots. For each station, time, position, and bottom depth were recorded at the start and the end of fishing (net on the seabed). The hours of fishing were always the same, 07:00–19:00, except June 1992, when two stations, with nine cod caught during each, were also sampled around midnight. The sampling protocol for the surveys is described by Magnussen (2002).

Cod age was determined from the otoliths. Total length (L) and ungutted weight (W) of each fish was measured to the nearest millimetre and gramme, respectively. The Fulton condition factor (K) was calculated as $K = W \times 10^5/L^3$.

Diet

Cod diet was determined based on the analysis of stomach contents. The stomachs were collected randomly immediately after the weight and length of the fish had been measured, then frozen on board; later, the contents were analysed ashore. Stomach fullness was assessed visually on a scale from 1 to 6 (1, empty; 2, little content; 3, half filled; 4, full; 5, distended; 6, everted). Stomach contents when present were sorted by separating the prey and identifying it to the lowest taxon feasible, quantified by weight and number. For each prey item, the extent of

Table 1. Number of stations and stomachs collected, and length information for the cod used for investigating stomach contents on the Faroe Bank.

Variable	5–8 June 1992	24 July 1992	11–17 April 1994	5–8 May 1995	26–29 March 1996	6–9 September 1996	21–25 March 1997	5–7 September 1997	19–22 March 1998	18–21 September 1998	All surveys
Number of stations	12	2	12	14	8	11	12	8	11	9	99
Number of stomachs	81	27	104	118	117	130	136	124	126	114	1 077
Fish length (cm)											
Average	85	87	80	76	81	83	84	88	87	85	83
Standard deviation	14	6	19	19	16	17	17	14	12	12	16
Minimum	46	72	41	41	44	22	39	58	66	33	22
Maximum	109	102	111	119	119	119	127	115	121	116	127
Fish age (years)											
Average	5.9	n/a	5.0	3.9	4.0	3.5	4.3	4.2	4.6	4.3	4.3
Standard deviation	1.7	–	2.4	2.2	1.9	1.6	2.0	1.7	1.7	1.5	2.0
Minimum	2	–	2	2	2	0	2	2	3	1	0
Maximum	10	–	9	10	10	9	16	11	14	13	16

n/a, not available.

digestion was measured on a scale from 1 to 5 (1, fresh; 2, digestion started, all species identifiable; 3, about half-digested, prey identifiable to taxon; 4, almost fully digested, only part of the prey identifiable; 5, fully digested, not identifiable). Hereafter, the term "fresh" is applied to all prey taxa, fish, and squid, with an assessed digestion of 1.

The mean partial fullness index (PFI) and total fullness index (TFI) of prey were calculated from

$$\mathrm{TFI} = \sum_{i=1}^{m} \mathrm{PFI}_i = \frac{1}{n}\sum_{j=1}^{n} \frac{w_{ij}}{L_j^3} \times 100$$

and stomach fullness index (SFI) from

$$\mathrm{SFI}_j = \frac{\sum_{i=1}^{m} w_{ij}}{L_j^3} \times 100,$$

where w_{ij} is the weight (g) of prey i in cod j, L_j the length (cm) of cod j, m the number of prey categories, and n the number of cod in the sample. SFI corresponds roughly to the percentage prey weight in relation to predator weight. As the spring surveys on the Faroe Bank take place during the main spawning season of cod, the calculation of SFI was based on predator length rather than weight, because fish length did not change whether or not the cod had spawned. The power of this length-based SFI was confirmed by comparing it with weight-based indices of the same fish; the correlation between the two indices was excellent ($r^2 = 0.99$).

Statistical analyses

Statistical analyses were performed on a SYSTAT 11 PC-program (SYSTAT, 2004). Temporal differences in length distribution, Fulton condition factor, fishing depth, and average weight of stomach contents (empty stomachs included) were tested by a Kruskal–Wallis test. Temporal and sex-specific differences in the proportion of empty stomachs were tested by a χ^2 test and variance analyses, and covariance analysis was used to test the effect of fish length on SFI and Fulton condition factor. The effects on SFI of year, time of day, depth of fishing, and fish length were tested using multiple regressions. Statistical tests were performed separately for spring and autumn surveys.

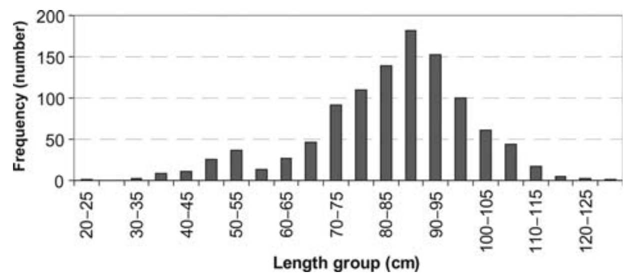

Figure 2. Size distribution of the cod ($n = 1077$) used in investigating the food and feeding habits on the Faroe Bank.

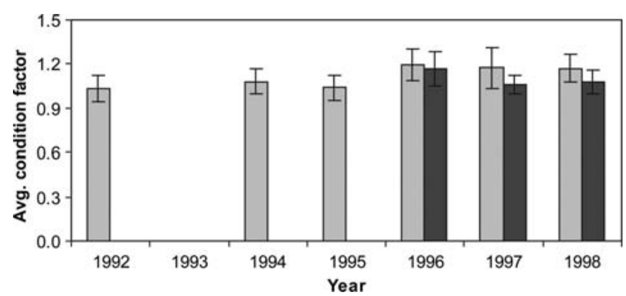

Figure 3. Average condition factor ($\pm$ s.d.) of Faroe Bank cod in spring (light grey) and autumn (dark grey).

Results

At the 99 trawl stations from which samples were collected, fishing depth varied from 91 to 209 m, with an average depth of 123 m (median 114 m; Figure 1). For the autumn surveys, there were no differences in fishing depth among surveys ($p = 0.742$), but in spring, there was a slight difference in depth ($p = 0.044$). For spring, it was the survey of July 1992 in particular that contributed to the difference. However, that survey consisted of just two stations: one at 98 m and the other at 102 m. Omitting those two stations, there was no statistical difference in fishing depth among the spring surveys ($p = 0.066$).

Condition factor

The cod used for investigating feeding habits on the Faroe Bank averaged 83 cm, 7151 g, and 4.3 years old (Figure 2, Table 1). The condition factors varied significantly during the time-series, for both spring and autumn surveys ($p < 0.001$; Figure 3). Average condition factor was highest during the years 1996–1998, 1.17–1.20 in spring and 1.06–1.17 in autumn. No significant differences were found in condition factor between seasons ($p > 0.05$; average 1.12 vs. 1.10). In three of the ten surveys (June and July 1992, and September 1998), condition factor decreased with fish length ($p < 0.008$), whereas it increased in four of the ten surveys: spring 1996, 1997, and 1998, and autumn 1998 ($p < 0.001$). For the other surveys, the condition factor did not change with fish length ($p > 0.08$).

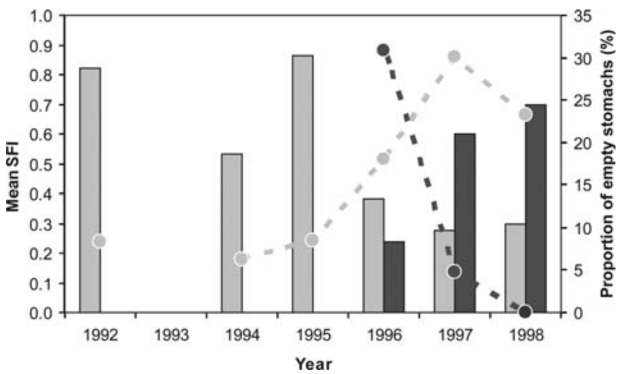

Figure 4. Median SFI of cod stomachs with food from the Faroe Bank in spring (light grey) and autumn (dark grey), and the proportions of empty stomachs (dashed lines).

Proportion of empty stomachs

This parameter varied significantly among years, in both spring ($p < 0.001$) and autumn ($p < 0.001$; Figure 4). Empty stomachs were fewest at the start of the time-series (6–9%), but then the proportion rose, and in autumn 1996 and again in spring 1997, almost one-third of the stomachs were empty. Feeding conditions subsequently improved and, during the last survey of the time-series in 1998, all 114 stomachs collected contained food. Overall, significantly more stomachs were empty in spring than in autumn (12 vs. 6%; $p < 0.001$). There was no difference in the proportion of empty stomachs among size groups of cod ($p > 0.08$; Table 2), or by sex in spring ($p > 0.50$) or autumn ($p > 0.18$).

Weight of stomach contents

The weight of stomach contents varied from year to year during spring surveys ($p < 0.001$), but not during autumn surveys ($p > 0.107$; Figure 5). It was highest in 1992, with an average food weight of 98 g per stomach. It then decreased gradually and was just 35 g in autumn 1996 and spring 1997. There was a strong negative correlation between the proportion of empty stomachs and the weight of their contents, in both spring ($r = -0.87$) and autumn ($r = -0.95$). Overall for the ten surveys, stomach contents averaged 58.3 g (median 27.6 g) for the 899 cod whose stomachs contained food.

Table 2. Proportion of empty stomachs and median/average values of SFI (s.d. in parenthesis) and PFI (s.d. in parenthesis) of stomachs with some food grouped by small (<70 cm), medium-sized (70–95 cm), and large (>95 cm) cod, the number of stomachs analysed, and the average age and length (with s.d. in parenthesis) of the predator.

						PFI			
Length category	*n*	Age (years)	Length (cm)	Empty (%)	SFI	Crustaceans	Fish	Squid	All taxa
Small	172	2.2 (0.6)	56 (10)	13	0.74/1.28 (1.4)	0.18/0.38 (0.46)	0.78/1.35 (1.5)	0.32/0.59 (0.65)	0.74/1.28 (1.40)
Medium	672	4.0 (1.2)	84 (7)	14	0.50/0.87 (1.2)	0.22/0.37 (0.45)	0.25/0.58 (1.0)	0.41/1.03 (1.65)	0.49/0.86 (1.21)
Large	230	6.8 (2.0)	102 (6)	19	0.49/1.02 (1.4)	1.30/0.28 (0.39)	0.33/0.78 (1.2)	0.46/1.05 (1.57)	0.45/1.02 (1.39)

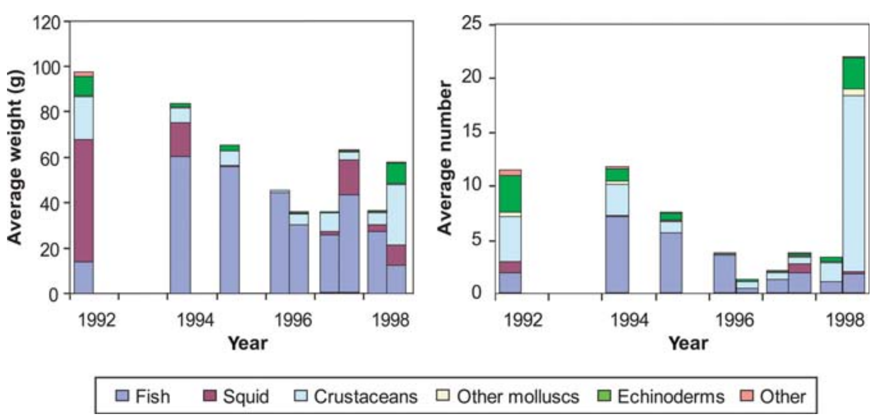

Figure 5. Average stomach contents by weight (left) and number (right) of principal food groups of cod on the Faroe Bank. For the last 3 years, double bars are shown: those to the right are for autumn and to the left for spring. Only stomachs containing food are included.

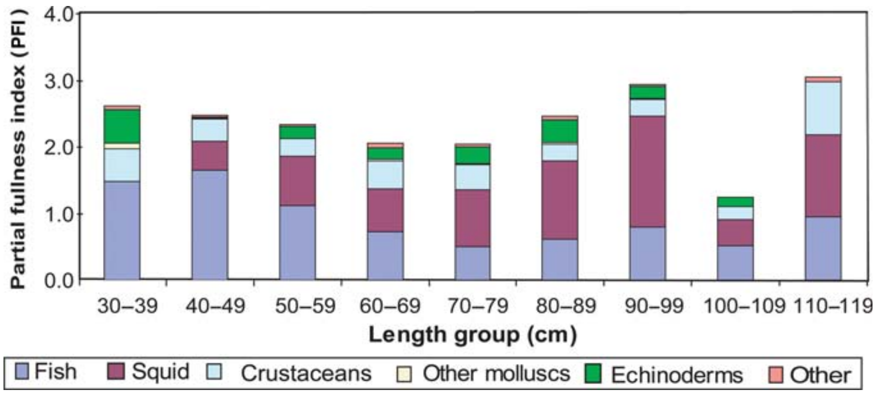

Figure 6. Stomach content and food composition of cod on the Faroe Bank, expressed as PFI values for the main prey groups by length of cod.

Stomach fullness index

As for the stomach contents, the SFI also varied significantly from year to year, in both spring ($p < 0.001$) and autumn ($p < 0.001$; Figure 4). The index peaked in July 1992, when 50% of the cod had stomach indices of 0.91 or higher, and was lowest in March 1997, when the median was 0.28. Comparing seasons, SFI values were significantly higher in autumn than in spring (median 0.54 vs. 0.33; $p < 0.005$), although the autumn surveys were only performed during the final 3 years of this time-series of surveys. The diet of cod shifted ontogenetically, with the highest SFI and PFI for the smallest cod ($p < 0.05$; Table 2). This shift was most obvious for the two prey groups fish and crustaceans, where the PFI varied significantly among size groups of cod ($p < 0.05$ and $p < 0.001$, respectively; Figure 6). For the other groups of prey, no significant variations were found in PFI among cod size groups ($p > 0.17$).

There were significant correlations ($p < 0.03$) between condition factor and SFI in just three of the surveys (June 1992, May 1995, and September 1998). Always, the fattest fish had the fullest stomachs. In terms of variation in the SFI, only a small percentage (10% in spring and 9% in autumn) could be explained by the following four parameters: year, hour of fishing, depth, and fish length. Of these, year was the only parameter that had a significant effect in both spring and autumn ($p < 0.001$). For two of the spring surveys, 1996 and 1997, the SFI increased significantly as cod size decreased ($p < 0.001$), but in autumn, fish length had no effect on the SFI ($p > 0.862$).

Diet

In all, 148 prey taxa were identified in cod stomachs during the ten surveys. Of these, 29 were found in at least 2% of the 1077 stomachs investigated (Table 3). The number of taxa identified varied dramatically between surveys, being lowest in July 1992 (22) and highest in September 1998 (79). However, even with a large number of different prey taxa, a few made up most of the diet. During the whole time-series, 29 prey taxa constituted between 67% (March 1998) and 96% (September 1997) of the diet by number, and between 77% (March 1997) and 95% (September 1997) of the total weight consumed.

Fish were the main food of cod on the Faroe Bank. Overall, fish made up 59% of the total weight eaten during the 10 surveys, but because of their large individual size, accounted for just 35% of the total by number (Table 3). Overall, fish were found in 82% of the stomachs with food. However, the portion of fish prey varied from year to year, being lowest in spring 1992, when fish made up only 13% of the weight consumed, and highest in spring 1996, when fish accounted for >97%. These two surveys were also those with the highest and lowest average stomach contents in the time-series, with 106 g in June 1992 and only 45 g per stomach in March 1996. Of the fish, lesser sandeel (*Ammodytes tobianus*) was the most common prey, contributing 78% of the fresh fish weight found in the cod stomachs. In addition to fresh lesser sandeel, the diet also consisted of partly digested sandeels, unidentifiable to species level. Including these prey too, sandeels (Ammodytidae) accounted for 90% of the fresh fish weight in the stomachs. The average length of fresh lesser sandeels consumed was 17 mm, and the average weight was 10 g. Of other fish species, haddock accounted for 4.3% of the diet by weight, Norway haddock (*Sebastes viviparus*) for 2.9%, and Norway pout (*Trisopterus esmarki*) for 1.5%. As prey, cod (i.e. cannibalism) were found in just one of the 1077 cod stomachs collected on the Faroe Bank, in just a single specimen.

In some years, squid (Cephalopoda) formed an important part of the diet (Figure 5). In June 1992, then again 1 month later, squid were found in 43 and 64% of the stomachs, respectively, constituting 54 and 60% of the diet by weight, respectively. Overall, for all the surveys, however, squid occurrence was just 13%, or 19% of the total food weight and 4% by number. Of the squid prey, *Loligo forbesi* dominated (94%) those identified. The average individual size of fresh *L. forbesi* was 36 g and 110 mm mantle length.

Crustaceans were the most numerous food items. Overall, they were recorded in 48% of the stomachs, constituting 44% of the prey items by number, but just 16% by weight (Table 3). On average, 3.4 crustaceans were found in each stomach. The proportion of crustaceans tended to vary during the period of study, being highest in September 1998 when 74% of the food items by number were crustaceans, i.e. 16.4 crustaceans per stomach on average. Of the crustaceans, *Atelecyclus rotundatus* dominated, contributing 29% by weight of freshly consumed crustaceans. Other notable crustaceans identified were *Hyas coarctatus*, 24% of the weight of crustaceans, and *Lithodes maja*, 11% by

Table 3. Diet composition of the main food items of cod on the Faroe Bank, ordered by taxon.

	Spring 1992			Autumn 1992			Spring 1994			Spring 1995			Spring 1996			Autumn 1996			Spring 1997			Autumn 1997			Spring 1998			Autumn 1998			Total for all surveys		
Food taxon	*F*	*n*	*w*	*F*	*n*	*w*	*F*	*n*	*w*	*F*	*n*	*w*	*F*	*n*	*w*	*F*	*n*	*w*	*F*	*n*	*w*	*F*	*n*	*w*	*F*	*n*	*w*	*F*	*n*	*w*	*F*	*n*	*w*
Hydrozoans																																	
Hydrozoa	8.1	0.4	0.1	4.0	0.5	0.1	3.3	0.4	0.0	1.9	0.1	0.0	–	–	–	1.1	–	0.0	1.1	–	0.0	1.7	–	0.0	4.5	–	0.1	21.9	–	0.6	4.9	0.1	0.1
Anthozoa	6.8	0.9	0.1	–	–	–	7.7	0.7	0.1	–	–	–	–	–	–	–	–	–	–	–	–	4.3	–	0.1	6.7	–	0.4	16.7	–	0.3	4.6	0.2	0.1
Scleractinia	–	–	–	–	–	–	–	–	–	7.4	–	0.1	2.1	–	0.1	6.7	–	0.1	5.3	–	0.2	–	–	–	–	–	–	–	–	–	2.3	–	0.0
Polychaetes																																	
Polychaeta	20.3	2.7	2.2	4.0	0.5	0.0	2.2	0.9	0.1	–	–	–	–	–	–	1.1	–	0.0	1.1	–	0.0	4.3	2.5	0.1	–	–	–	1.8	0.1	0.0	2.9	0.7	0.4
Molluscs																																	
Gastropoda	13.5	1.5	0.2	–	–	–	3.3	0.3	0.0	–	–	–	1.0	–	0.0	2.2	0.9	0.1	–	–	–	1.7	–	0.0	1.1	–	0.0	3.5	0.1	0.0	2.5	0.3	0.0
Bivalvia	6.8	0.5	0.1	–	–	–	12.1	1.1	0.3	6.5	0.4	0.1	–	–	–	4.4	0.9	0.2	–	–	–	13.7	1.1	0.2	13.5	1.4	0.2	23.7	0.4	0.2	8.9	0.6	0.1
Loligo forbesi	29.7	5.3	50.1	64.0	19.1	60.1	3.3	0.5	16.2	–	–	–	–	–	–	2.2	0.9	0.5	1.1	–	0.1	23.1	22.9	24.6	5.6	1.4	8.3	10.5	0.6	14.8	9.6	3.0	17.8
Crustaceans	*(74)*	*(35)*	*(20)*	*(68)*	*(46)*	*(16)*	*(57)*	*(25)*	*(8)*	*(44)*	*(14)*	*(11)*	*(18)*	*(4)*	*(3)*	*(38)*	*(49)*	*(12)*	*(36)*	*(30)*	*(23)*	*(23)*	*(16)*	*(5)*	*(48)*	*(54)*	*(14)*	*(95)*	*(74)*	*(46)*	*(48)*	*(44)*	*(16)*
Crustacea spp.	9.5	0.4	0.2	28.0	–	2.6	5.5	0.8	0.2	17.6	0.4	1.2	7.3	–	1.6	13.3	15.5	1.2	13.7	–	3.7	10.3	–	1.5	19.1	2.0	2.7	59.6	0.6	8.4	18.2	0.8	2.2
Meganyctiphanes sp.	–	–	–	–	–	–	–	–	–	0.9	0.6	0.0	–	–	–	–	–	–	–	–	–	3.4	0.9	0.0	–	–	–	32.5	35.1	7.0	4.6	12.9	0.9
Pandalus montagui	1.4	0.1	0.0	4.0	0.5	0.1	3.3	0.3	0.1	0.9	0.1	0.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	26.3	13.2	3.8	3.9	4.9	0.5
Lithodes maja	–	–	–	–	–	–	1.1	0.1	0.9	2.8	0.5	1.4	–	–	–	1.1	–	0.0	5.3	1.0	12.2	1.7	0.9	0.6	3.4	1.0	2.7	7.0	1.1	1.2	2.5	0.6	1.5
Munida sp.	2.7	0.2	0.0	–	–	–	12.1	4.7	2.1	–	–	–	4.2	1.1	0.2	8.9	6.9	1.1	7.4	14.6	3.3	0.9	0.2	0.1	3.4	4.7	1.6	19.3	1.9	2.4	6.3	2.3	1.0
Galathea intermedia	5.4	1.7	0.3	8.0	2.7	0.2	17.6	3.1	0.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.4	0.8	0.2
Galathea sp.	2.7	0.2	0.0	8.0	2.7	0.5	6.6	1.1	0.3	–	–	–	–	–	–	–	–	–	–	–	–	8.5	4.8	0.5	9.0	6.1	0.8	39.5	5.1	3.3	8.0	2.7	0.6
Galathea nexa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6.0	2.7	0.4	7.9	7.1	0.9	15.8	3.4	4.1	3.5	1.7	0.6
Hyas coarctatus	25.7	16.1	6.5	28.0	9.8	1.6	4.4	0.5	0.3	–	–	–	–	–	–	2.2	4.3	0.7	2.1	1.5	0.3	3.4	0.9	0.2	–	–	–	5.3	0.8	1.1	4.8	3.0	1.3
Hyas sp.	4.1	0.3	0.1	–	–	–	1.1	0.1	0.1	1.9	0.3	0.1	–	–	–	1.1	0.9	0.1	1.1	0.5	0.1	–	–	–	–	–	–	14.0	0.9	1.2	2.6	0.4	0.2
Inachus leptochirus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	0.9	0.2	4.5	2.7	1.1	13.2	2.6	4.7	2.2	1.1	0.7
Atelecyclus rotundatus	40.5	10.1	9.1	20.0	4.4	2.5	2.2	0.7	0.2	–	–	–	–	–	–	–	–	–	–	–	–	4.3	3.4	1.2	–	–	–	12.3	1.2	3.0	6.1	2.3	2.0
Liocarcinus holsatus	12.2	2.2	1.5	28.0	23.5	6.4	15.4	11.9	1.2	–	–	–	–	–	–	–	–	–	–	–	–	0.9	0.5	0.3	1.1	0.3	0.1	27.2	2.5	1.5	6.9	3.7	0.8
Liocarcinus turbeculatus	–	–	–	4.0	0.5	0.2	1.1	0.1	0.2	13.9	3.0	1.1	3.1	0.8	0.4	8.9	13.8	6.0	4.2	3.0	0.4	–	–	–	–	–	–	–	–	–	3.5	0.7	0.6
Echinoderms																																	
Ophiura sp.	1.4	0.1	–	–	–	–	2.2	0.3	0.0	1.9	8.5	3.4	–	–	–	8.9	12.9	1.4	8.4	6.6	0.4	1.7	4.8	0.4	10.1	12.5	1.3	55.3	13.1	15.2	10.4	7.0	2.6
Amphiura sp.	27.0	29.2	9.0	16.0	11.5	4.2	8.8	8.8	1.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.5	5.7	1.8
Fish	*(62)*	*(16)*	*(13)*	*(48)*	*(20)*	*(20)*	*(80)*	*(60)*	*(72)*	*(85)*	*(75)*	*(86)*	*(92)*	*(96)*	*(97)*	*(77)*	*(31)*	*(85)*	*(87)*	*(59)*	*(72)*	*(92)*	*(50)*	*(68)*	*(92)*	*(30)*	*(75)*	*(77)*	*(8)*	*(21)*	*(82)*	*(35)*	*(59)*
Pisces spp.	40.5	5.8	2.0	16.0	3.8	1.6	23.1	3.5	1.4	23.1	1.1	3.7	31.3	4.0	9.9	54.4	3.4	43.1	41.1	2.5	8.4	26.5	0.2	6.8	36.0	2.0	22.4	45.6	0.8	5.9	34.1	2.3	8.1
Ammodytes sp.	20.3	3.3	1.7	4.0	1.1	0.0	11.0	3.1	1.3	–	–	–	10.4	12.1	15.4	14.4	17.2	13.0	46.3	40.9	40.0	65.0	48.5	57.5	55.1	21.3	34.9	10.5	0.6	2.8	25.1	7.3	15.6
Ammodytes tobianus	13.5	4.7	5.3	28.0	12.0	5.1	49.5	49.6	63.3	61.1	70.1	72.9	59.4	76.3	63.7	3.3	0.9	9.4	2.1	11.6	4.9	–	–	–	–	–	–	–	–	–	20.7	21.1	26.1
Callionymus lyra	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.1	1.0	0.7	0.9	0.2	0.1	6.7	1.4	0.8	8.8	0.6	1.3	2.1	0.3	0.3
Pleuronectidae	1.4	0.3	0.1	–	–	–	4.4	0.4	0.4	8.3	1.3	2.0	4.2	0.8	0.6	2.2	3.4	0.8	3.2	1.0	2.7	–	–	–	6.7	3.0	2.0	24.6	1.4	3.8	6.2	1.0	1.2
Other groups																																	
Stones	1.4	0.1	0.0	–	–	–	–	–	–	9.3	–	0.2	4.2	–	0.1	11.1	–	0.5	1.1	–	0.0	3.4	–	0.1	3.4	–	0.5	6.1	0.0	0.1	4.4	0.0	0.1
106 other food items	100	13.7	11.5	100	7.1	14.7	100	7.1	8.6	100	13.6	13.8	100	4.8	8.0	100	18.1	21.9	100	15.7	22.5	100	4.3	5.0	100	33.1	19.1	100	13.7	13.0	100	12.4	12.3
Total number of taxa	58			22			49			31			23			34			33			40			38			79			148		
Total number of specimens	937			183			1 065			800			354			116			198			437			296			2 494			6 880		
Total weight (g)	7 875			1 785			7 616			7 063			4 350			3 219			3 360			7 339			3 250			6 596			52 454		

Only taxa found in >2% of all stomachs from the ten surveys analysed are included; taxa with less presence are listed as "other food items". *F*, percentage of stomachs containing the food listed; *n*, percentage by number; *w*, percentage by weight. The italicized values in parenthesis for crustaceans and fish are the pooled values for all items belonging to those taxa. Dashes indicate the absence of a taxon in that survey.

weight. The small flying crab (*Liocarcinus holsatus*) contributed 12% of the crustacean diet by weight but as much as 30% by number, so was the most frequent crustacean species eaten by cod on the Faroe Bank.

Discussion

Cod on the Faroe Bank are clearly mainly piscivorous, although in some years *L. forbesi* and different species of crustacean contributed a substantial part of the diet. On the Faroe Bank, cod live on the shallowest part, down to 200 m, although their preferred depth seems to be ~120 m (Magnussen, 2002). In that habitat, the seabed consists mainly of shell-sand and sand, with a water temperature of ~8°C in March and almost 11°C in September (Magnussen, 2007). The Faroe Bank is well known for delivering large cod, reflected also in the size distribution of the cod analysed here. The average cod length from all surveys was 83 cm, a result in accord with the size distribution in the population (Faroe Marine Research Institute, unpublished data).

On average, ten stations were sampled during each survey; at first sight, this sample size may seem to be low. From a stomach-sampling programme in the Barents Sea, the diet varies much more between stations than within stations (Bogstad *et al*., 1995), but compared with the Barents Sea, the Faroe Bank is very small, covering an area shallower than 200 m of just 45 × 90 km (3500 km^2; Magnussen, 2002). Therefore, the Faroe Bank ecosystem is more homogenous than that of the Barents Sea, and samples from fewer stations are needed for accurate analysis of diet.

Fish were the preferred food of cod on the Faroe Bank, contributing 59% of the diet by weight, on average. Of the fish, sandeels (especially lesser sandeels) were the most common species and made up 78% of the fresh fish weight consumed. This large proportion is in accord with earlier findings of cod feeding on the Bank. Comparing the diet of Faroese cod, Steingrund (2009) found that sandeels were more commonly eaten on the Faroe Bank than on the nearby Faroe Plateau, and Rae (1967) found sandeels to be the main diet of cod on the Faroe Bank, occurring in 70% of the stomachs, which also was the highest proportion of sandeel he found for Faroese cod.

In all, crustaceans were found in 48% of the stomachs in the present investigation, making up 16% by weight of the diet. A similar contribution was recorded by du Buit (1982), who found crustaceans in 51% of the stomachs, 25% of the diet by weight. The presence of crustaceans in the diet in the current investigation is comparable with the findings of Steingrund (2009) for cod on the Faroe Bank, who recorded crustaceans in ~15% of the stomach contents in spring and 27% in autumn. Moreover, those levels are comparable with the results reported for other Arcto–Boreal ecosystems, where the portion of crustaceans eaten by cod varies between 10 and 25% of total biomass (Pálsson, 1994).

The importance of cephalopods as prey for cod on the Faroe Bank varied considerably during this time-series. In some surveys, they were found in 64% of the stomachs, making up 60% of the diet by weight. In other years, the cephalopods were a negligible part of the diet. This changing cephalopod presence agrees with other reported results of the feeding habits of cod on the Faroe Bank, especially the low levels found in some years in the present study. Neither Rae (1967) nor Steingrund (2009) found cephalopods to be a part of cod diet on the Faroe Bank, and in du Buit's (1982) investigation, only one cephalopod was reported.

It is well known that Atlantic cod are generalist predators whose diet changes to include the most abundant prey in their habitat at any time (Hoines and Bergstad, 1999; Hanson and Chouinard, 2002; Link *et al*., 2009). In the southern Gulf of St Lawrence, cod predation can change from principally invertebrates to piscivory, mainly Atlantic herring (*Clupea harengus*). This shift was most obvious for the largest cod (60–75 cm) and consistent with observed changes in the abundance of Atlantic herring in the ecosystem (Hanson and Chouinard, 2002). Therefore, the variation in the importance of cephalopods as prey for cod on the Faroe Bank is probably related to their fluctuating abundance in the area. In the present investigation, a strong positive correlation ($r^2 = 0.71$) was found between *L. forbesi* caught in the trawl and its presence in cod stomachs.

Although just a few prey species contributed most of the diet, 148 prey taxa in all were identified. Compared with other areas, this is quite a large number. Rae (1967) mentioned 72 prey taxa consumed by cod on Faroese grounds; of these, there were just 12 on the Faroe Bank. For cod off southwestern Norway, 32 taxa made up most of the diet (Hoines and Bergstad, 1999). In contrast, Mattson (1990) reported 191 species eaten by cod over a soft sublittoral seabed off the west coast of Sweden. However, comparing stomach analyses among ecosystems needs to be done with caution because the number of prey species reported will depend largely on the way that the diet analyses are undertaken. Basically, the number of prey species increases as the number of stomachs investigated increases. Furthermore, the taxonomic composition of any fish diet varies in both space and time, and changes are also ontogenetic. Additionally, the taxonomic scope of the analyses may be chosen subjectively and arbitrarily, and it often depends on the taxonomic knowledge of the investigator and the level of care applied. With these factors taken into consideration, the reports of different authors may not be fairly comparable (Mattson, 1990).

The present investigation revealed that cannibalism was practically non-existent for cod on the Faroe Bank. Of the 1077 stomachs investigated from the ten surveys during the years 1992–1998, cod as prey were found just once, and in just a single cod predator. Therefore, the level of cannibalism is likely much lower for cod on the Faroe Bank than in other North Atlantic areas, where 0.6–2.5% of cod prey on cod, making up 4–6% of the diet by weight (Pálsson, 1994). It is well known that cannibalism in cod depends on fish size, of both predators and prey (Bogstad *et al*., 1994; Pálsson, 1994; Hanson and Chouinard, 2002; Link *et al*., 2009). For cod as prey, very few are <40 cm (Bogstad *et al*., 1994; Hanson and Chouinard, 2002), so a primary reason for cannibalism being rare on the Faroe Bank is probably because few cod on the Bank are of that size. In the eight demersal surveys conducted on the Faroe Bank during the years 1994–1998, only 37 cod were <40 cm (Faroe Marine Research Institute, unpublished data) and hence potential prey for larger cod.

The proportion of empty stomachs found reflects the foraging activity and hence the feeding conditions for cod on the Faroe Bank. An abundance of prey would naturally generate fewer empty stomachs and higher stomach fullness. Generally, both the proportion of empty stomachs and stomach fullness vary considerably for cod in the North Atlantic (Hoines and Bergstad, 1999; Hanson and Chouinard, 2002; Michalsen *et al*., 2008). For cod on the Faroe Bank, there was clear temporal variation, both seasonally and annually. As expected, stomach fullness was greatest during those years when there were few empty stomachs. Overall, the portion of empty stomachs varied from 0 to 30%, with an average of 15% for all ten surveys. This level is consistent with earlier findings, 16% of cod on Faroese grounds (Rae, 1967) and ~15% of cod on the northeastern US continental shelf (Link and Garrison, 2002) having empty stomachs. In two of the three comparable years in our investigation, more stomachs were empty in spring than in autumn, probably because of spawning, because cod appetite seems to decline before and during spawning (Fordham and Trippel, 1999; Michalsen *et al.*, 2008).

For the whole time-series analysed here, the average stomach contents weighed 58.3 g. However, using absolute weight of stomach contents to compare between ecosystems may be misleading, because the fish analysed often differ in size. Generally, the quantity of food fish consume depends on their size: bigger fish need more food than smaller fish. Hence, more stomach contents by weight do not necessarily mean better feeding conditions. A more suitable metric for comparison of an ecosystem's feeding conditions is SFI, in which the weight of stomach contents is standardized with respect to fish size.

The current investigation shows that the diet of cod shifts ontogenetically, with stomach fullness higher for cod <70 cm, in accord with the results of Steingrund (2009), who found the smallest cod on the Faroe Bank to have the greatest stomach fullness, in both spring and autumn. In March, his results showed that the SFI declined from 1.4 for smaller cod (45–55 cm) to 0.5 for larger cod (>85 cm) and, in September, from 5.7 for cod 25–35 cm long to ~0.6 for cod >85 cm. Stomach fullness being greater for cod <70 cm could therefore be the reason why the growth of Faroe Bank cod is pronounced during the first 3 years of life (Faroe Marine Research Institute, unpublished data). The suggestion of particularly good feeding conditions for small cod on the Faroe Bank is further supported by the diet composition of that size of cod, i.e. mainly fish, of which sandeels are most common. Sandeels are characterized by their greater nutrient quality (Pedersen and Hislop, 2001) than crustaceans and other invertebrates, which tend to be the main diet of smaller cod in other ecosystems (Link *et al.*, 2009).

To conclude, fish (especially sandeels) are the main food of cod on the Faroe Bank. However, in some years, the squid *L. forbesi* and different species of crustacean form a notable part of the diet. The diet of cod shifts ontogenetically, with stomach fullness greater and nutrient quality of prey higher for smaller cod; cannibalism, however, is practically nonexistent there.

Acknowledgements

I thank my colleagues at the Faroe Marine Research Institute for support in the practical aspects of this project and my colleagues Robert Brown and Hóraldur Joensen for useful comments and advice on an earlier version of the manuscript.

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