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Seasonal variation of the diet of cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.) at a herring spawning ground.

by

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ABSTRACT

The paper describes diet variation of cod and haddock at a spawning ground of the Norwegian Spring Spawning Herring. Samples were collected at bi-monthly intervals through a one-year period, including during and following the spawning season of herring in March-April

The significance of herring and herring eggs is analysed in relation to the diet of the two demersal species during the remainder of the year. Both species show strong diet shifts when herring or herring eggs appear in the area.

INTRODUCTION

In boreal waters, interactions between oceanic long-range migrating fish populations and resident coastal communities may be most pronounced during and after the short periods of the year when the oceanic populations concentrate at coastal sites to spawn. To the coastal communities, long-range migrants may constitute major seasonal pulses of prey, predators and/or competitors.

The significance of spawners and spawning products as food for coastal fish populations is considered in this paper. Little quantitative information exists on the utilization by the coastal populations of this input of seasonal biomass of prey. This paper describes the diet of cod and haddock at a herring spawning ground and focuses on intraspesific diet shifts during and after the relatively short herring spawning season.

As study site was chosen a historically important spawning area of the Norwegian Spring Spawning Herring off the island of Karmøy in southwestern Norway (Bergstad et al. 1991a) (Figure 1). Comprehensive studies of herring and the resident fish communities are conducted in this area, and cod and haddock are among the most abundant predators at the herring grounds (Bergstad et al. 1991b). The herring spawns over a period of 5 - 6 weeks in March and April at this location.

Cod and haddock of all sizes (Figure 2) occur in the area, and both species appear to spawn there. There is some uncertainty as to how stationary the cod population is. Tag-recapture experiments during the spawning season of herring indicated that the rate of emigration to offshore areas, e.g. the North Sea, was very low (own data, unpubl.). The majority of recaptures were reported from sites close to where the fish were tagged. Periodic immigration of non-resident cod of unknown origin is often claimed by local fishermen, however.

Seasonal sampling of stomachs form the basis of this analysis. Multivariate ordination techniques were used to define major patterns in the data, such as differences between size-groups and seasons.

MATERIAL AND METHODS

Sampling

The descriptions of diets were based on collections of stomach contents at roughly bi-monthly intervals, either from fish caught by shrimp trawl from R/V Håkon Mosby (See Bergstad et al. 1991b) or by Danish seine from a commercial fishing vessel (Table 1). The research vessel worked the area during the herring spawning season in March 1991 and further in July. Data from other times came from Danish seine samples, but were collected in the same areas as those sampled by trawls.

Stomachs of haddock were all fixed in 4% seawater solution of formaldehyde buffered by borax, then after fixation transferred to 70% ethanol. Cod samples from the research vessel were also treated in this way. The Danish seine samples of cod, however, were processed fully onboard, i.e. prey were sorted to species, counted and measured, but not weighed. All haddock samples and the cod stomachs from the research vessel were processed in the laboratory, and prey weights were recorded in addition to numbers and sizes.

Analysis

Eigenvector ordination techniques, either Principal Component Analysis (PCA) or Detrended Correspondence Analysis (DCA) (Hill 1979, Gauch 1982), were found efficient with these types of data. Both techniques are tools for identifying underlying gradients which explain most of the variation in the dataset.

The choice between PCA and DCA depends on the length of the first gradient, i.e. the one explaining the most of the variation. A recommended procedure is initially to run a DCA, then a PCA if the length of the first DCA axis is less than 3 standard deviation units (ter Braak and Prentice,1988).

RESULTS

Stomach contents were examined from 1068 haddock and 821 cod. A total of 113 prey taxa were recorded from the haddock stomachs, while for cod the number of prey was much lower with 71 prey taxa recorded.

Stomach contents of two size categories of haddock and cod in terms of percentage by weight, percentage by numbers and percentage frequency of occurrence of different prey taxa are given in Tables 2 and 3. Separate tables are given for samples from within the herring spawning season and from other times of the year. Mean weight per stomach was calculated based on all stomachs, empty ones included, within each size group. All stomachs from areas shallower than 100 m off the island of Karmøy were pooled.

Seasonal and ontogenetic variation in diet composition were analysed simultaneously. For haddock, Principal Component Analysis (PCA) was used because of the very short gradient of the first DCA-axis (1.9 SD). Detrended Correspondence Analysis (DCA) was used for cod. Figure 3 shows the scores for all length groups of haddock in all seasons except the herring spawning season. Since the diet was very different in March and April compared with other periods, data from these months were excluded from the ordination.

Estimated eigenvalues of the first four ordination axes were 0.44, 0.25, 0.11 and 0.08 respectively. Ordination axes 1 and 2 explained 69% of the variation in the diet. Axis 1 reflected the varying presence of *Ammodytes,* particularly pronounced in June and to some extent in December. The different sampling periods were separated along the second axis, indicating that seasonal variation in the diet was more important than ontogenetic variation. However, the smallest individuals (i.e less than 20 cm TL) were separated from the larger ones. This length group was only sampled in July, and the diet was dominated by polychaetes. Separation along the second axis seems to reflect occurrence of epibenthic prey at the lower part and more benthic prey at the upper. In February and October the different length groups of haddock appear close, indicating a similar diet.

Analysis of the stomach contents of cod from trawl stations in March and July with DCA are shown in Figure 4. The basis for this analysis were stomach contents in terms of percentage by weight. The estimated eigenvalues of the first four DCA axes were 0.90, 0.37, 0.09 and 0.08. This means that these ordination axes explained 38.5, 15.9, 4.0 and 3.4 per-cent of the variation. Considering the plot of predator groups, it appears that the first axis represents a length gradient with the largest size groups of cod at left. This is also reflected in the prey plot were the largest prey are found to the left (e.g. herring and sandeel). The second axis seem to represent the difference in season, with March predator groups and prey categories with relatively low values. In both seasons the proportion of fish in the diet increased with increasing predator length, and in March only cod larger than 50 cm (TL) ate adult herring. Herring eggs were mainly fed on by the intermediate length groups i.e 30-39 and 40-49 cm (TL). Cod smaller than 30 cm (TL) had a relatively similar diet in both periods, but the differences increased with increasing predator length.

The food composition in different seasons.

Haddock.

The composition of some main prey groups of each size group of haddock in different seasons are shown graphically in Figure 5. The most outstanding feature is the predominance of herring eggs in the herring spawning season, particularly in the haddock larger than 25 cm. In these length groups herring eggs contributed from 35 to 100 per-cent in terms of weight, and frequency of occurrence values were high. In March and April polychaetes and small crustaceans were the most important prey for haddock smaller than 25 cm (Figure 5a).

Data from February and October were pooled because the PCA indicated close similarity. In these periods epibenthic prey, i.e echinoderms and crustaceans, were the most predominant prey taxa (Figure 5c). Among the crustacean prey, isopods, mainly *Cirolana borealis*, and crabs were most significant. Their proportion in terms of weight varied from around 2 to 19 per-cent. The most dominant echinoid species were ophiurids (6-29%), *Echinocyamus pusillus* (2-11%) and *Strongylocentrotus droebachiensis* (0-21%).

Sandeel, *Ammodytes* spp. contributed most by weight to the diet of haddock in June (Figure 5c), and also for the largest length group (larger than 50 cm in length) in December. It contributed from 38 to 61 per-cent by weight, but frequency of occurrence values were low, i.e from 6 to about 17 per-cent.

In July, polychaetes were important in all length groups, but most significant in the smallest size group (15-19 cm in length), with a proportion of 54 per-cent in terms of weight (Figure 5b). Ophiurids and other epibenthic prey also contributed more to the diet in this period. All length groups above 20 cm (TL) seemed to have a rather similar diet in this period.

In December polychaetes were the predominant food for haddock smaller than 50 cm (Figure 5c). The proportion in terms of weight of polychaetes were around 60 per-cent in these two length groups, and nearly all stomachs with contents contained this prey taxon. The largest length group (larger than 50 cm in length) deviated from this with only 14 per-cent polychaetes. However, also in this size group the frequency of occurrence of polychaetes was high (50%).

Cod

The most outstanding feature of the average food composition of cod was the remarkable shift in the diet in March (the herring spawning season). In this period sandeel, which was at other times very important, was almost absent from the diet. Herring and herring eggs took over as the predominant food.

In March caridean shrimps and other crustaceans were the most important prey of cod smaller than 30 cm (Figure 6a). The most dominant caridean shrimp genus was *Pandalus* spp., with a proportion of 13.4 and 31.4 per-cent in terms of weight in these length groups. In the two intermediate size groups (30-39 and 40-49 cm in length) herring eggs dominated. The contribution of herring eggs to the diet were 58.7 and 71.6 per-cent in these two length groups, and the frequency of occurrence was relatively high, i.e. 27.8 and 40.7 per-cent. Cod larger than 50 cm had a very high proportion of adult herring in the diet, from around 75 to 100 per-cent in terms of weight. The frequency of occurrence of herring varied from about 56 to 100 per-cent in these length groups.

In July sandeel were the predominant food of cod larger than 30 cm (Figure 6b). In all these length groups the proportion of sandeel was higher than 68 per-cent, and the frequency of occurrence was high, i.e. from 54.2 to 100 per-cent. Only the smaller cod (< 20 and 20-29 cm in length) ate, as in March, mainly caridean shrimps and other crustaceans.

The Danish seine material did not show any significant seasonal variation. In all seasons, sandeel dominated the stomach contents. Their contribution in terms of percentage by numbers varied from around 70 to 99.5 in all well represented size groups. Figure 6c shows the average food composition in terms of percentage by numbers for cod larger than 30 cm, further illustrating the dominant role of sandeel in the diet of cod throughout the year.

Stomach content weight.

The quantity of the stomach contents, empty stomachs included, were analysed for both haddock and cod. Figure 7 shows mean weight of contents of haddock of different length groups in different seasons. Above 30 cm (TL), all length groups in March and April had significantly more stomach contents than corresponding length groups in other seasons (Kruskal-Wallis test, $p < 0.05$). The amount of stomach contents of the smallest length group was not significantly different in March and July.

In March and July the mean stomach contents of cod showed the same pattern as for haddock (Figure 8), but the only length group which had a statistically significant higher mean weight in March was the intermediate length group, i.e. 30 - 49 cm in length ($p < 0.05$). The differences were not significant for the other length groups.

Thus the length groups of cod and haddock which preyed upon herring eggs had more contents in March than at other times when herring eggs were unavailable.

DISCUSSION

The seasonal sampling of co-occurring cod and haddock revealed both inter- and intraspecific dietary differences. The multivariate analyses indicated differences between size groups and seasons. Of the two predators, cod was the typical piscivore, feeding primarily on sandeel in this area. Only the small cod (TL < 30 cm) fed mostly on other prey than sandeel, i.e. benthic and benthopelagic crustaceans. Haddock, however, fed on epibenthic invertebrates and infauna, fish prey were generally unimportant. Only in June did sandeels appear to play an important role. These overall patterns are similar to those found in other areas were these species co-occur (Daan,1973; Jones,1978; Langton and Bowman,1980; Pàlsson,1983).

In March, both cod and haddock apparently responded immediately and strongly to the presence of a new food resource, either herring or herring eggs. The diet shifts in favour of these new and seasonal resources were pronounced, in some predator length groups virtually complete.
This shows that both predators are able to respond quickly and take advantage of a resource which may only be abundant over a relatively short time interval.

Some intraspecific patterns appeared. Haddock smaller than 30 cm TL did not feed as strongly on herring eggs as did the larger ones. For cod, intermediate sized fish fed on eggs, whereas large fish (TL > 50 cm) preyed on adult herring. This was the case even though the intermediate sized cod were rather strongly piscivorous outwith the herring season.

Both predators seemed to have greater amounts of stomach contents in March-April compared with the other sampling periods. This may reflect a higher feeding rate during the herring season. However, as yet no direct estimates of consumption were made.

In the years studied, some 15 - 20,000 tonnes of herring visited the Karmøy spawning ground (Bergstad et al. 1991 a). Although this may be a very small biomass compared with historical records, it probably represents a major short-term input to this rather limited area and must also substantially increase the overall abundance of fish. In 1991 and 1992 the first major herring concentrations appeared in the last week of February (Bergstad 1991 a, unpubl. data), and by the third week of March most had retracted from the main grounds. Eggs were still found in haddock stomachs two weeks into April. At the spawning grounds, cod and haddock would thus be able to feed on herring for about 4 weeks and herring eggs for at least 8 weeks.

An obvious next step would be quantify the present and potential energetic significance of herring and herring eggs for cod and haddock in this area. Thus far, no such estimates were made. Stomach samples from species other than cod and haddock indicate that herring eggs may be consumed by several other species. Saithe (*Pollachius virens*) and pollack (*Pollachius pollachius*) were the more abundant species feeding on herring eggs.

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Table 1. Vessels, sampling periods, gears and material collected.

				NUMBER OF STOMACHS	
SHIP	FROM	TO	GEAR	HADDOCK	COD
M/S Bjørg Evy	22/10-90	25/10-90	D.seine	91	70
M/S Bjørg Evy	13/12-90	18/12-90	"	62	68
M/S Bjørg Evy	11/2-91	14/2-90	"	118	101
R/V Håkon Mosby	4/3-91	26/3-91	TRAWL	448	177
M/S Bjørg Evy	22/4-91	25/4-91	D.seine	110	106
M/S Bjørg Evy	11/6-91	13/6-91	"	50	102
R/V Håkon Mosby	6/7-91	11/7-91	TRAWL	172	154
M/S Bjørg Evy	13/10-91	17/10-91	D.seine	17	43

Table 2. Haddock (Melanogrammus aeglefinus). Stomach contents in terms of percentage by weight (%W), percentage by numbers (%N) and percentage frequency of occurrence (%F) of different prey taxa. Entries at higher taxonomic level include contents identified at that level only.

Prey taxon	Herring spawning season						Outside herring spawning season					
	<30 cm			>30 cm			<30 cm			>30 cm		
	%W	%N	%F	%W	%N	%F	%W	%N	%F	%W	%N	%F
Chlorophyta										0.41	0.00	0.2
Hydroida										0.00	0.02	0.2
Physophora hydrostatica				0.00	0.04	0.4				0.05	0.17	0.7
Polychaeta	7.20	8.13	25.5	0.25	5.06	17.1	14.11	12.61	50.0	20.08	9.67	48.3
Aphroditidae				0.02	0.11	0.4				1.58	0.19	2.9
Polynoidae	13.88	1.06	5.5	0.00	0.04	0.2	7.89	1.30	7.9	0.33	0.13	1.7
Hesionidae	0.07	1.06	5.5	0.00	0.61	1.1	1.80	0.43	2.6	0.12	0.44	3.9
Nereidae	0.03	0.71	1.8	0.02	0.14	0.7				1.89	0.44	2.4
Nereis	0.11	0.35	1.8	0.01	0.07	0.4				1.11	0.11	1.7
Nephtyidae										0.52	0.03	1.0
Glyceridae				0.00	0.04	0.2				0.07	0.08	0.7
Oweniidae										0.98	1.04	0.2
Sabellariidae										0.03	0.09	0.7
Ampharetidae				0.00	0.07	0.4	0.04	0.43	2.6	0.45	0.72	3.4
Pectinaria										0.03	0.05	0.7
Gastropoda	0.54	2.47	1.8	0.00	0.07	0.4				0.07	0.35	2.0
Archaeogastropoda										0.01	0.03	0.2
Littorina										0.02	0.05	0.2
Eulimidae				0.00	0.22	0.9	0.08	0.43	2.6	0.01	0.08	1.0
Natica alderi				0.00	0.08	0.4				0.02	0.04	0.5
Buccinum undatum				0.00	0.07	0.4						
Cylichna	0.37	1.06	5.5	0.00	0.18	1.1				0.02	0.14	2.0
Polyplacophora	0.04	0.35	1.8	0.01	0.47	2.9	0.29	0.87	5.3	0.05	0.30	3.7
Lepidopleurina				0.00	0.04	0.2						
Lepidopleurus asellus	0.11	0.35	1.8	0.02	1.18	4.8	2.36	3.48	15.8	0.30	1.58	10.5
Bivalvia	0.44	1.06	3.6	0.03	0.93	4.4	1.76	3.48	15.8	1.56	1.67	14.9
Chlamys				0.01	0.32	1.8				0.43	0.56	5.3
Lima	0.30	1.06	5.5	0.09	2.19	8.8	0.79	4.35	10.5	0.86	1.65	12.7
Cardiidae	0.11	0.35	1.8	0.01	0.47	2.4				0.09	0.13	1.5
Cardium	0.16	0.71	3.6	0.01	0.36	1.1						
Parvicardium minimum	1.73	4.59	12.7	0.00	0.14	0.7	0.64	0.87	5.3	0.11	0.32	3.2
Ensis				0.00	0.04	0.2						
Tellina				0.00	0.07	0.2				0.02	0.14	1.7
Mya	0.26	0.35	1.8	0.00	0.07	0.4	0.93	0.87	5.3	0.20	0.16	2.2
Rossia				0.10	0.07	0.2	1.23	0.43	2.6	0.55	0.03	0.5
Crustacea	2.08	3.89	10.9	0.05	0.79	4.0	1.16	1.30	7.9	0.72	0.60	9.8
Ostracoda				0.00	0.04	0.2	0.02	0.87	5.3			
Calanus finmarchicus	0.00	0.35	1.8				0.01	1.30	5.3			
Mysidacea										0.00	0.02	0.2
Cumacea	0.00	0.71	3.6							0.00	0.11	1.7
Isopoda				0.00	0.25	0.2				0.00	0.02	1.7
Cirolana borealis	6.40	25.80	20.0	0.15	2.45	11.4	1.01	1.74	10.5	4.68	4.30	21.7
Astacilla longicornis										0.00	0.02	0.2
Arcturella dilatata							0.01	0.43	5.3			
Amphipoda				0.00	0.04	0.2				0.00	0.02	0.2
Gammaridea	0.64	14.49	29.1	0.02	3.95	11.9	0.92	14.78	42.1	0.38	2.84	22.2
Ampeliscidae	0.14	0.35	1.8	0.01	0.54	1.8	0.10	0.87	5.3	0.15	0.76	3.4
Gammaridae										0.02	0.06	0.7
Haustoriidae				0.00	0.36	0.2						
Epimeria cornigera										0.00	0.02	0.5
Hyperiidea							0.01	0.43	2.6	0.01	0.11	1.2
Parathemisto				0.00	1.08	0.9				0.00	0.08	0.5
Parathemisto abyssorum				0.02	3.84	2.9				0.00	0.03	0.7
Caprellidae							0.01	0.43	5.3	0.01	0.11	0.7
Euphausiidae				0.00	0.07	0.4				0.00	0.02	0.2
Thysanoessa										0.01	0.03	0.5
Decapoda	2.73	1.06	5.5	0.06	1.04	2.0	2.98	1.30	7.9	1.13	0.44	5.6

Table 2. Haddock (Melanogrammus aeglefinus). Continued

Prey taxon	Herring spawning season						Outside herring spawning season					
	<30 cm			>30 cm			<30 cm			>30 cm		
	%W	%N	%F	%W	%N	%F	%W	%N	%F	%W	%N	%F
Caridea	3.08	3.18	10.9	0.10	2.01	8.6	1.12	1.30	7.9	0.99	3.06	14.1
Hippolytidae				0.00	0.14	0.7				0.83	2.33	2.2
Spirontocaris										0.14	0.02	0.2
Spirontocaris pusiola				0.00	0.04	0.2				0.27	0.57	1.5
Pandalidae				0.00	0.04	0.2						
Pandalus				0.05	0.68	3.3				0.16	0.05	0.7
Pandalus borealis	3.68	0.35	1.8	0.08	0.29	1.5						
Pandalus montagui				0.09	0.18	0.9				0.82	0.17	2.0
Pandalina				0.07	2.80	2.9	4.74	0.43	2.6	0.07	0.09	1.0
Crangonidae				0.01	0.04	0.2				0.01	0.02	0.2
Crangon				0.03	0.22	0.2				0.22	0.06	1.0
Crangon allmanni				0.02	0.11	0.4				0.20	0.03	0.5
Anomura				0.00	0.04	0.2				0.02	0.05	0.7
Paguridae	0.03	0.35	1.8	0.00	0.14	0.4				0.18	0.68	3.4
Pagurus bernhardus							4.41	0.43	5.3			
Pagurus pubescens				0.00	0.07	0.2				0.03	0.02	0.2
Anapagurus laevis				0.01	0.29	0.4				0.07	0.19	0.5
Munida	3.23	0.35	1.8	0.00	0.07	0.4	0.30	0.43	2.6	0.43	0.09	0.7
Munida sarsi										0.01	0.05	1.2
Galathea				0.03	0.25	0.9	0.43	1.30	7.9	0.00	0.02	0.2
Galathea strigosa										0.01	0.02	0.2
Galathea intermedia										0.01	0.03	0.2
Brachyura	0.91	0.71	3.6	0.02	0.18	1.1	0.53	0.43	2.6	0.95	0.38	3.9
Hyas coarctatus				0.01	0.11	0.2				0.38	0.16	2.2
Carcinus maenas				0.00	0.04	0.2				0.03	0.05	0.5
Macropipus				0.02	0.14	0.9	0.85	0.43	2.6	0.89	0.36	3.9
Macropipus depurator										0.19	0.05	0.7
Macropipus holsatus				0.02	0.07	0.4				1.15	0.30	3.7
Macropipus pusillus										0.64	0.17	1.7
Echinodermata										0.16	0.00	0.7
Asteroidea				0.01	0.14	0.7	0.02	0.43	2.6	0.61	0.72	8.3
Astropecten irregularis							1.23	0.43	2.6	0.11	0.05	0.7
Solaster										0.02	0.02	0.2
Ophiuroidea										0.01	0.05	32.0
Ophiurida	2.36	6.01	20.0	1.63	32.82	25.9	11.72	10.00	21.1	10.60	19.05	17.8
Ophiura				0.13	6.10	8.1	0.94	3.91	5.3	1.91	9.44	2.6
Ophiura sarsi				0.01	0.68	1.3				0.18	0.47	0.2
Ophiura affinis				0.01	0.11	0.7				0.02	0.06	0.2
Ophiura texturata										0.08	0.02	0.2
Ophiopholis aculeata				0.52	7.86	13.2	3.02	2.17	7.9	2.74	2.90	12.9
Amphiuridae				0.02	0.18	1.1				0.04	0.03	0.2
Ophiothrix fragilis				0.12	0.61	2.4				1.27	0.50	3.7
Echinoidea	0.46	3.18	7.3	0.07	1.76	6.8	7.46	10.00	26.3	5.69	5.75	27.3
Echinus				0.08	1.36	5.5	0.17	0.43	2.6	1.77	2.27	11.7
Strongylocentrotus droebachiensis				0.01	0.36	0.9				1.23	1.12	5.1
Echinocyamus pusillus	1.51	14.49	30.9	0.12	11.80	22.2	2.86	13.48	34.2	2.20	17.49	44.6
Loveniidae										2.01	0.11	1.7
Cucumaridae				0.01	0.11	0.7				0.01	0.02	0.2
Chaetognatha										0.01	0.03	0.2
Teleostei	3.53	1.06	5.5	1.04	0.50	3.1	14.36	1.30	7.9	2.34	0.35	4.4
Clupeidae										0.52	0.22	2.0
Clupea harengus egg	25.43		5.5	93.92		68.6						
Ammodytes				0.01	0.07	0.4				4.70	0.19	1.5
Ammodytes marinus										7.68	0.11	0.5
Buenia jeffreysii										0.16	0.09	0.2
Pleuronectidae				0.00	0.04	0.2						
Indeterminatus	18.42		61.8	0.76		22.6	7.72		50.0	6.17		39.8
No. of stomachs examined	62			496			38			470		
No. of empty stomachs	7			41			0			60		
Mean weight of contents (g)	0.76			13.83			0.48			2.22		

Table 3. Cod (Gadus morhua). Stomach contents in terms of percentage by weight (%W), percentage by numbers (%N) and percentage frequency of occurrence (%F) of different prey taxa. Entries at higher taxonomic level include contents identified at that level only.

Prey taxon	Herring spawning season						Outside herring spawning season					
	<30 cm			>30 cm			<30 cm			>30 cm		
	%W	%N	%F	%W	%N	%F	%W	%N	%F	%W	%N	%F
Polychaeta	4.29	11.59	28.3	0.01	0.81	2.7	1.83	3.36	8.3	0.05	0.17	1.0
Aphroditidae										0.03	0.06	0.2
Polynoidae	0.13	0.61	2.2									
Hesionidae							0.10	0.84	2.1			
Nereidae										0.07	0.06	0.2
Nephtyidae	1.86	3.05	4.3									
Ampharetidae	0.09	5.49	2.2							0.01	0.06	0.2
Bivalvia	0.06	0.61	2.2							0.00	0.17	0.7
Chlamys										0.00	0.06	0.2
Rossia	6.81	0.61	2.2							0.67	0.06	0.2
Rossia macrosoma										0.21	0.06	0.2
Octopodida										0.00	0.06	0.2
Crustacea	1.31	0.61	10.9	0.02	0.20	1.8	2.95	0.84	12.5	0.31	0.28	1.9
Copepoda							0.02	0.00	4.2			
Isopoda										0.00	0.06	0.2
Cirolana borealis	0.17	0.61	2.2	0.14	8.27	3.5				0.60	4.04	4.0
Amphipoda	0.10	0.61	2.2							0.00	0.06	0.2
Euphausiacea										0.00	0.06	0.2
Euphausiidae										0.00	0.57	0.5
Decapoda	0.07	0.61	2.2	0.05	0.81	4.4	16.41	24.37	29.2	1.61	0.74	2.4
Penaeida										0.00	0.06	0.2
Caridea	8.97	42.07	52.2	0.37	22.58	24.8	19.33	30.25	27.1	0.58	1.94	3.8
Hippolytidae				0.00	0.81	1.8						
Pandalus	26.19	12.80	13.0	0.16	5.44	5.3	7.00	2.52	6.3	0.28	0.23	0.7
Pandalus borealis				0.04	0.40	1.8				0.00	0.11	0.2
Pandalus montagui	1.71	1.22	2.2	0.77	9.68	14.2				0.37	0.34	1.2
Pandalina	1.80	10.37	15.2	0.06	9.48	8.8	1.94	9.24	10.4	0.07	1.20	1.0
Crangon allmanni				0.02	0.20	0.9						
Anomura	2.91	0.61	2.2	0.02	0.20	0.9						
Calocaris macandrea	1.20	0.61	2.2									
Paguridae										0.06	0.06	0.2
Lithodidae										0.00	0.06	0.2
Lithodes maja										0.04	0.23	1.0
Munida										0.70	0.85	2.6
Munida sarsi				0.01	0.20	0.9				0.57	0.34	1.2
Galathea	0.78	1.83	6.5	0.03	1.41	4.4						
Galathea strigosa										0.04	0.06	0.2
Brachyura				0.20	1.21	5.3				1.19	1.37	5.0
Hyas coarctatus	0.09	0.61	2.2	0.04	0.81	2.7	2.61	2.52	6.3	2.12	1.71	6.4
Atelecyclus rotundatus										1.42	0.63	1.4
Cancridae										0.00	0.06	0.2
Cancer pagurus										0.00	0.11	0.2
Carcinus maenas				0.06	0.20	0.9	0.00	3.36	2.1	0.00	0.85	1.9
Macropipus	0.29	0.61	2.2	0.04	2.02	6.2				0.04	0.11	0.5
Macropipus depurator				0.04	0.60	2.7						
Macropipus holsatus	2.31	2.44	2.2	0.04	0.40	0.9				0.06	0.06	0.2
Macropipus pusillus										0.11	0.23	0.2
Ophiuroidea										0.00	0.23	0.2
Ophiurida				0.01	0.40	1.8	0.14	0.84	2.1	0.15	0.46	0.2
Ophiopholis aculeata				0.07	4.64	2.7				0.09	0.57	0.7
Ophiothrix fragilis										0.09	0.06	0.2
Echinoidea										0.00	0.06	0.2
Echinus				0.00	0.20	0.9						

Table 3. Cod (Gadus morhua). Continued

Prey taxon	Herring spawning season						Outside herring spawning season					
	<30 cm			>30 cm			<30 cm			>30 cm		
	%W	%N	%F	%W	%N	%F	%W	%N	%F	%W	%N	%F
Teleostei	17.35	1.83	6.5	2.07	4.03	16.8	29.44	7.56	18.8	2.12	2.16	8.3
Clupea harengus				81.53	14.72	42.5						
Clupea harengus egg	19.94		8.7	9.77		18.6						
Lophius piscatorius										0.00	0.11	0.5
Pollachius virens										0.00	0.46	1.7
Melanogrammus aeglefinus										0.00	0.06	0.2
Trisopterus esmarkii				0.12	0.40					0.30	0.91	3.3
Merlangius merlangus										0.00	0.06	0.2
Sebastes viviparus										3.18	0.06	0.2
Eutrigla gurnardus										0.00	0.06	0.2
Myoxocephalus scorpius										0.00	0.11	0.2
Ammodytes				2.51	6.65	8.0	16.83	13.45	12.5	63.26	75.64	77.4
Ammodytes marinus				1.79	3.23	3.5				19.43	1.37	1.9
Buenia jeffreysii	0.53	0.61	2.2				1.18	0.84	2.1			
Pleuronectoidei										0.00	0.06	0.2
Scophthalmus rombus										0.00	0.23	0.2
Pleuronectidae										0.17	0.11	0.5
Microstomus kitt										0.00	0.06	0.2
Indeterminatus	1.05		6.5				0.22		2.1			

No. of stomachs examined	51	126	55	589
No. of empty stomachs	5	13	7	168
Mean weight of contents (g)	1.98	79.04	1.10	-

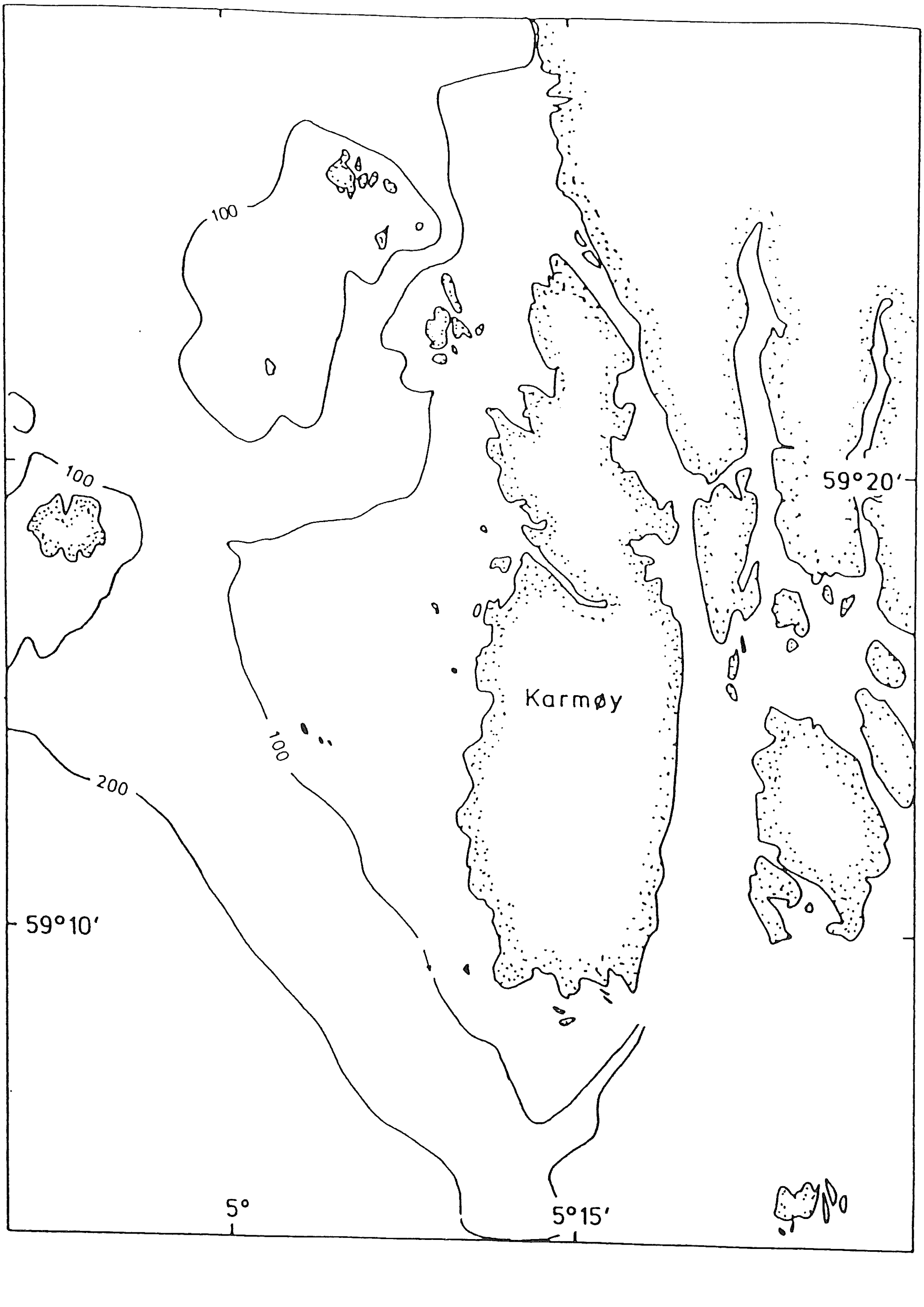

Figure 1. Bathymetric map of the area off the island of Karmøy. Trawl stations from the area shallower than 100 m.

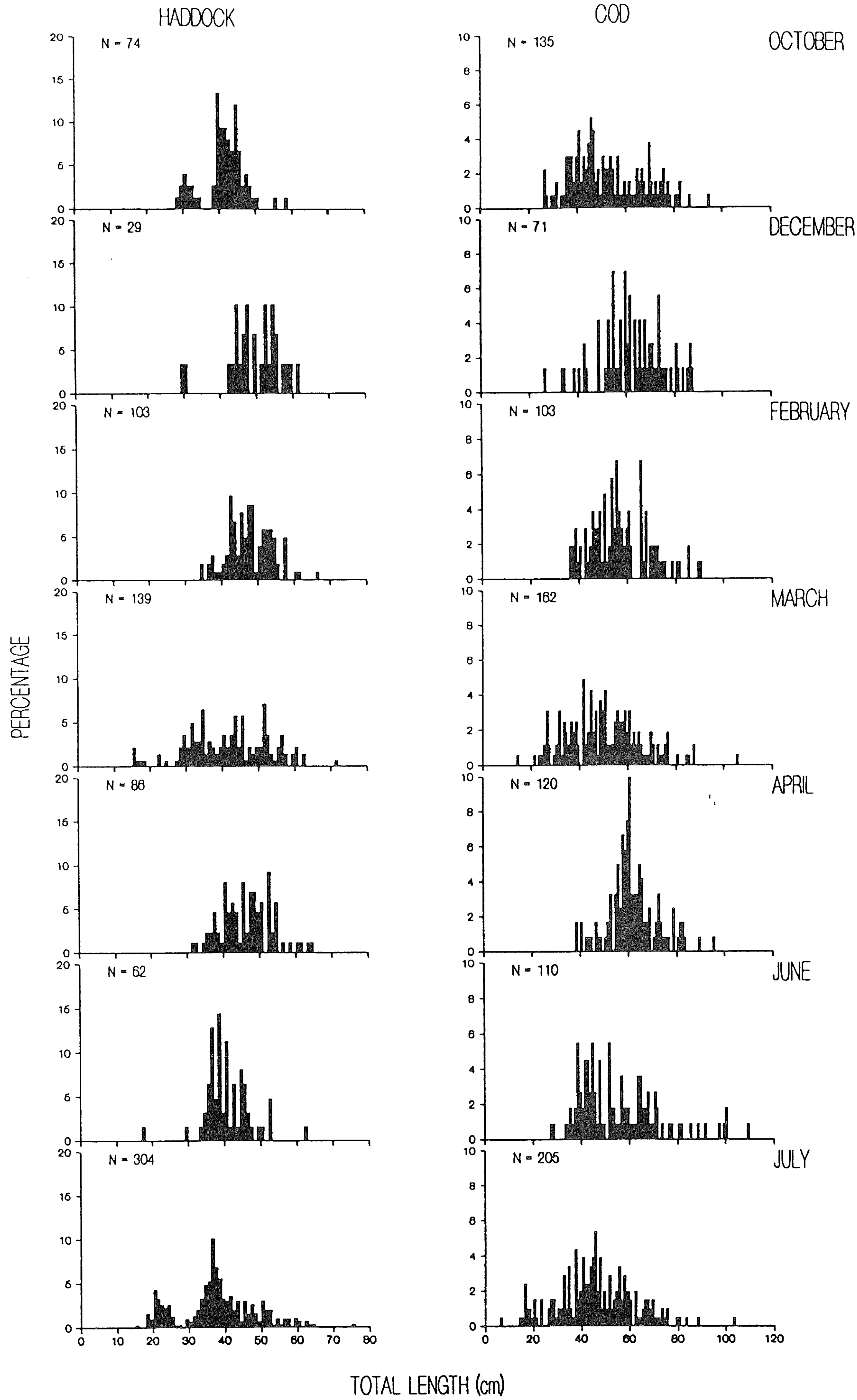

Figure 2. Length frequency distributions of cod and haddock in different seasons. N - number of fish.

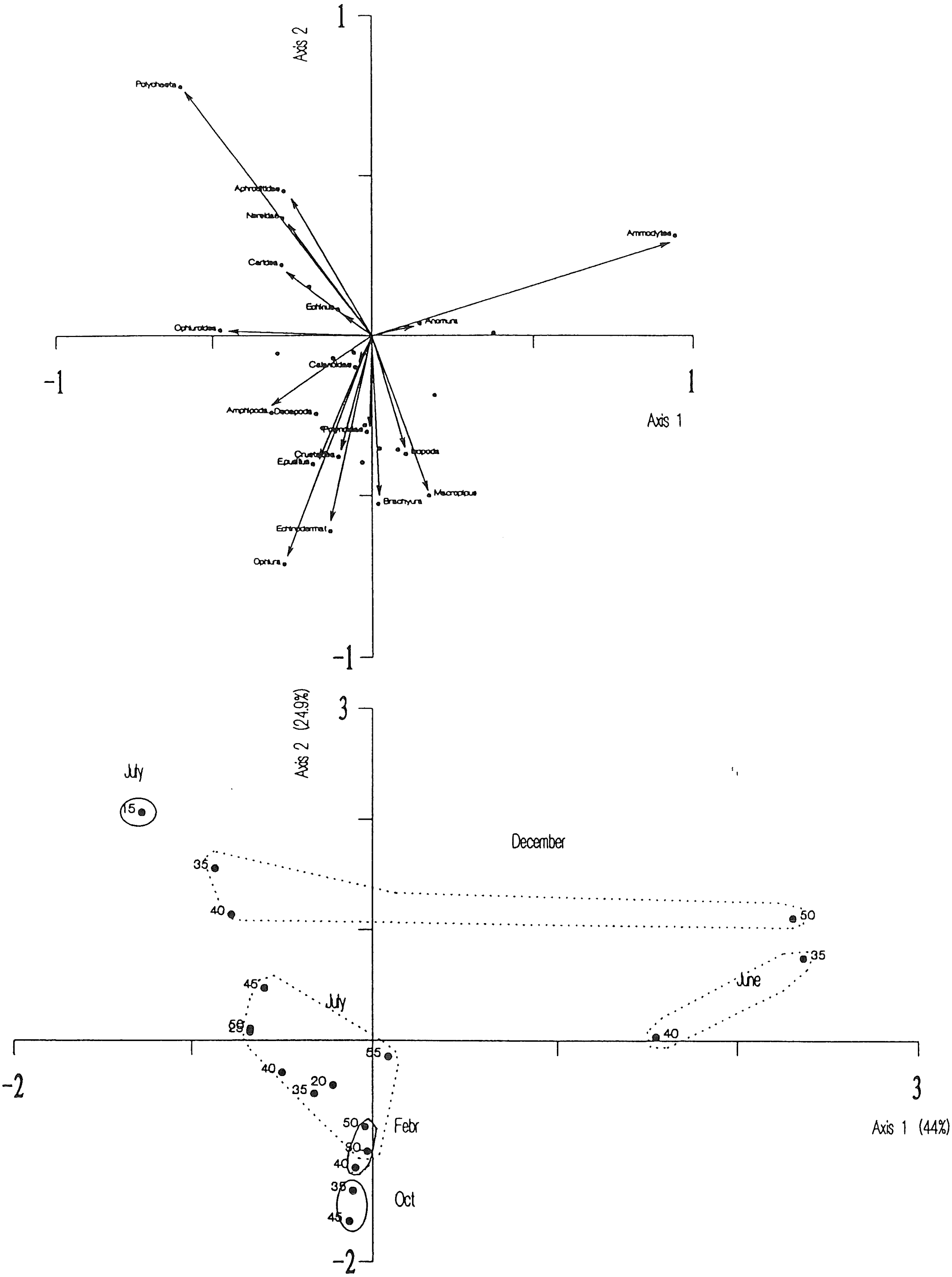

Figure 3. Principal Component Analysis of prey and predator groups of haddock outside the herring spawning season. Prey scores (upper) and predator scores (lower) on the two first ordination axes. Numbers mark lower limit of predator lengthgroups.

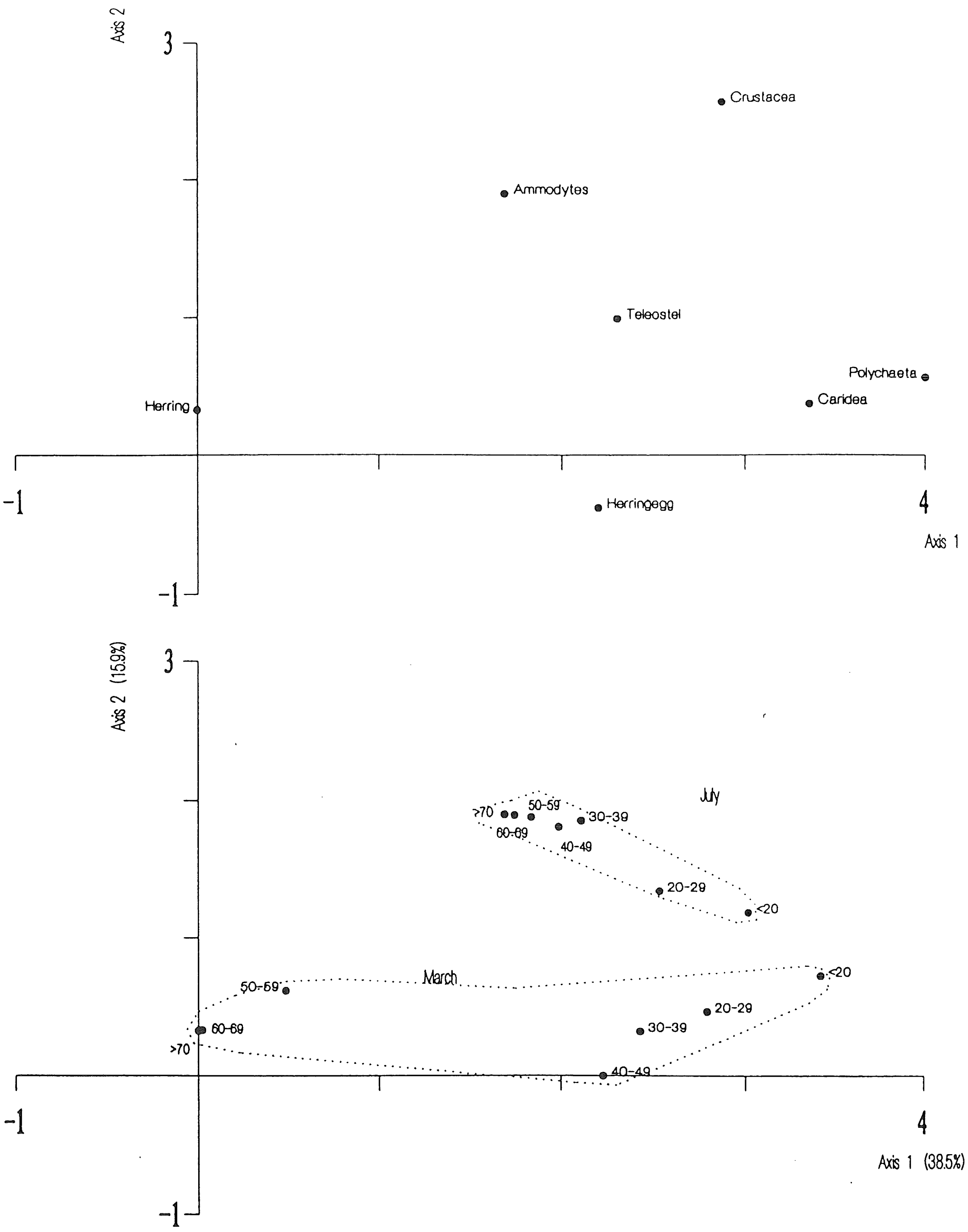

Figure 4. Detrended Correspondence Analysis of prey and predator groups of cod in March and July. Prey scores (upper) and predator scores (lower) on the two first ordination axes (SD-units).

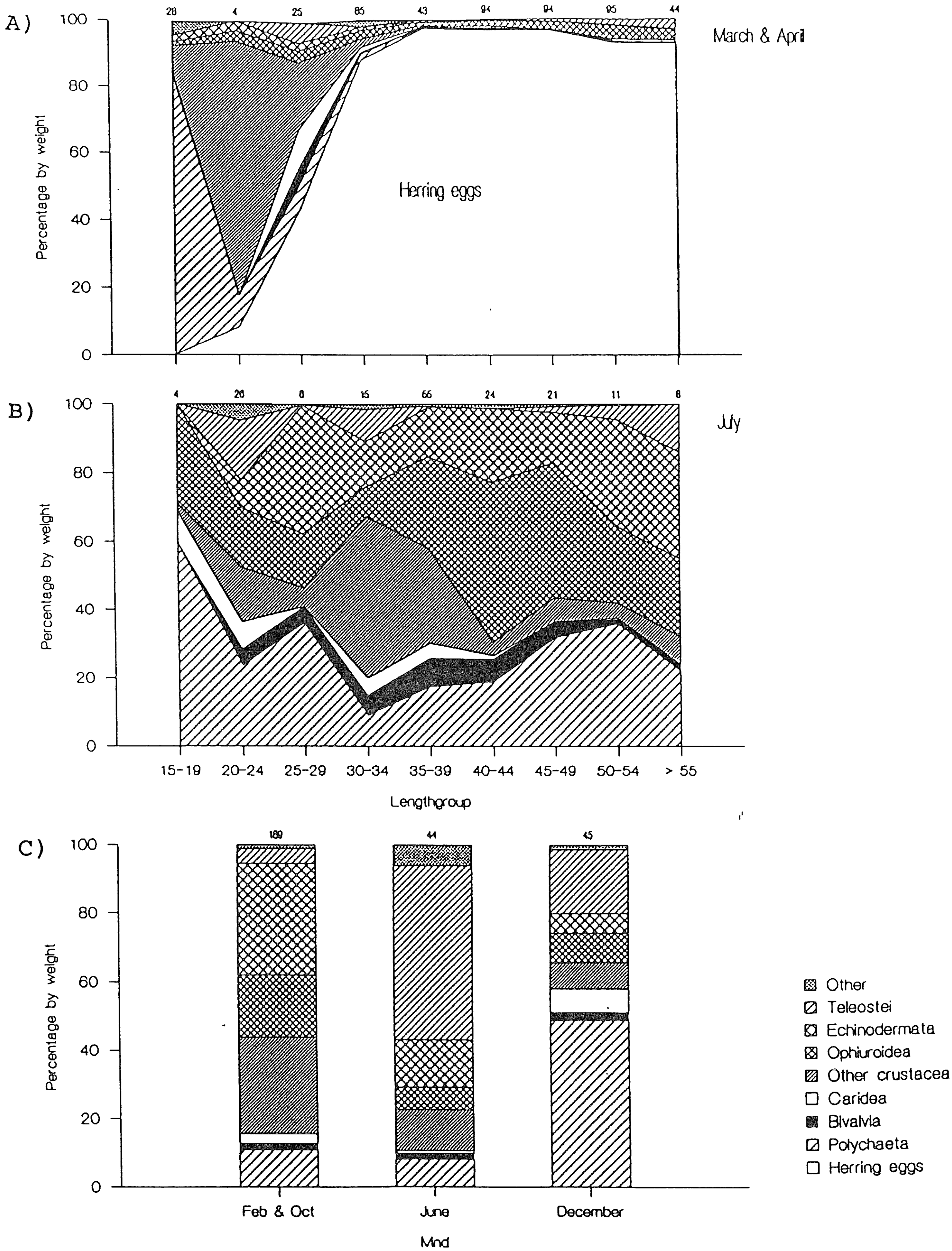

Figure 5. The composition of the food of haddock (weight percentages), in relation to the predator length (cm) in March and April, and July. The lengthgroups (only haddock larger than 35 cm) were pooled in the other periods. Number of stomachs with contents in each group marked at the top of the figures.

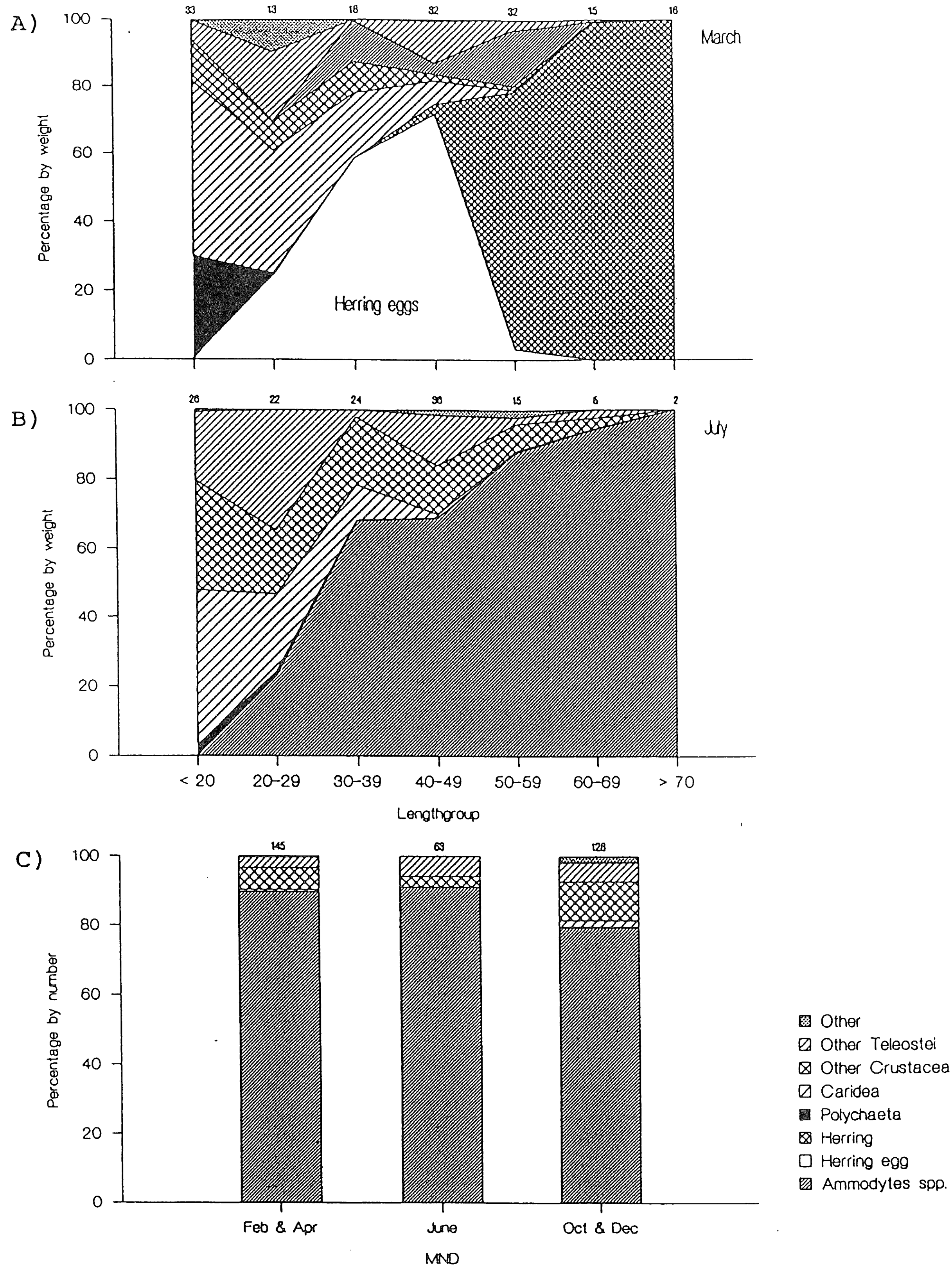

Figure 6. The composition of the food of cod (weight percentages), in relation to the predator length (cm) in March and July. The lengthgroups (only cod larger than 35 cm) were pooled and the food composition in percentage by number in the other periods. Number of stomachs with contents in each group marked at the top of the figures.

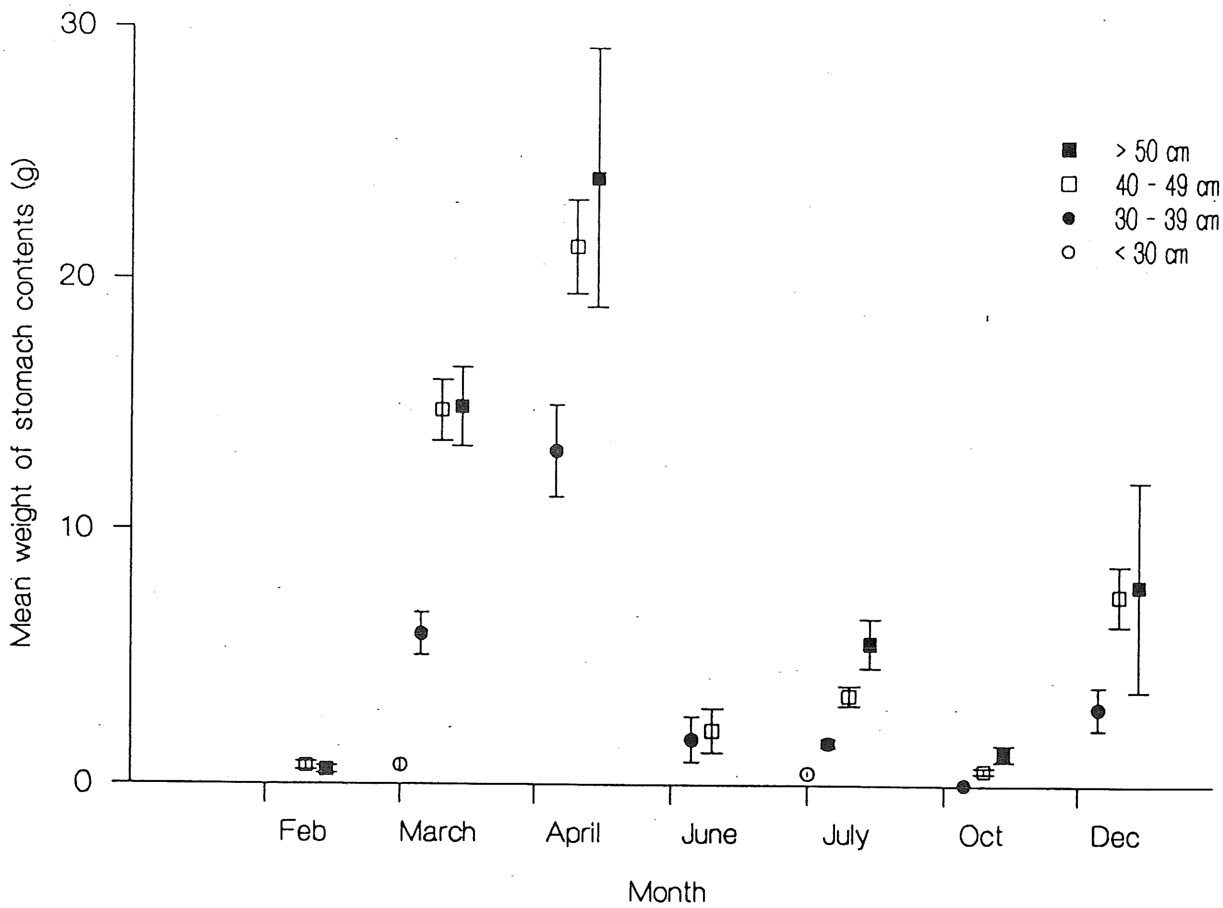

Figure 7. Seasonal variation in the average quantity of stomach contents of different length classes of haddock (weight in g). Vertical bars represent standard error of the mean.

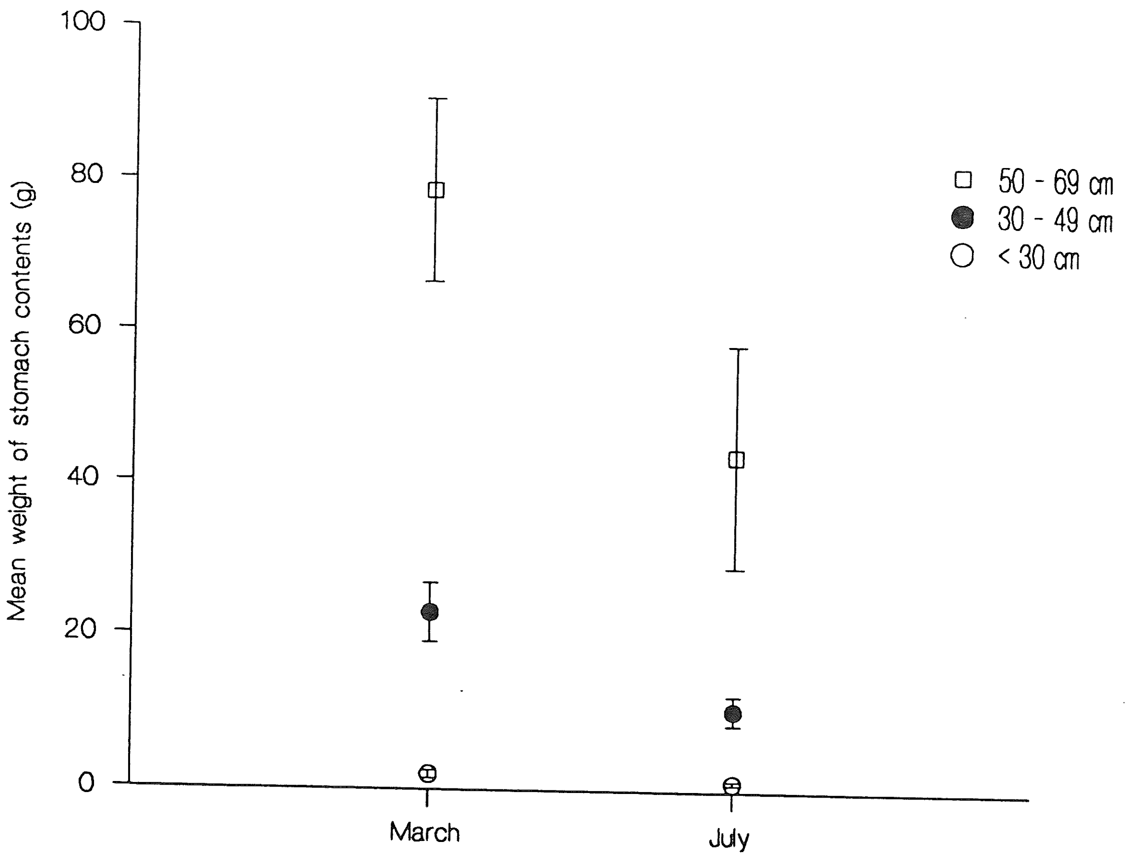

Figure 8. Variations in stomach contents quantity of different length classes of cod in March and July (weight in g). Vertical bars represents standard error of the mean.