J. Cons. int. Explor. Mer, 40: 101–111. 1982

# Food and feeding habits of cod from the Balsfjord, northern Norway during a one-year period

Anders Klemetsen

Institute of Biology and Geology, University of Tromsö, N-9001 Tromsö, Norway

The stomach contents of cod sampled by bottom trawl nine times in one year from three stations in the Balsfjord (69°N) were analysed. The possibility that the results were biased due to the cod feeding in the trawl net was discarded. In all 72 different animal taxa were recorded in the food. Of these 11 taxa made up the principal prey of cod in the fjord: deep water prawn *Pandalus borealis,* capelin *Mallotus villosus,* and small krill *Thysanoessa* spp. were the most important. The others were the polychaete *Nephtys* sp., the mysids *Erythrops* sp. and *Michteimysis mixta,* the amphipods *Arrhis phyllonyx, Halirages fulvocinctus,* and *Rhachotropis macropus,* the krill *Meganyctiphanes norvegica,* and herring *Clupea harengus.* Krill was probably the only prey taken in midwater. The relative importance of the prey and also the diversity of food in the cod stomachs varied between the stations. Food diversity was lowest at the mid-fjord station. This was probably due to smaller environmental variations, a lesser edge effect, and less influence of adjacent prey communities on this large and deep trawling ground. The fullness of the stomachs showed no seasonal trend and was not consistent between stations. Neither spawning nor the polar darkness seemed to influence food intake.

## Introduction

This study deals with several aspects of the food and feeding habits of cod, *Gadus morhua,* from the Balsfjord, northern Norway. It is part of a research programme on this fjord undertaken by the University of Tromsö.

Owing to the dominant rôle of the Arcto-Norwegian cod in the country's commercial fisheries the main Norwegian research effort has been concentrated on this stock. The numerous local populations, commonly designated as coastal cod, have received much less attention. Our knowledge of the biology of these local cod stocks is therefore limited. This is undesireable because their economic importance is likely to increase in forthcoming years.

Earlier studies on the food of cod (see for instance Brown and Cheng, 1946; Powles, 1958; Popova, 1963; Zatsepin and Petrova, 1939; Rae, 1967a; Daan, 1973; Arntz, 1974; Bowman, 1975) invariably show that the results from one area cannot be applied to cod from other areas except in a very general way. Because earlier results from the Balsfjord were sparse and concerned 0 to 2-group fish only (Wiborg, 1948; 1949), more extensive studies were called for in the fjord. An analysis of the food of cod was therefore included early in the programme.

The main aim of the study was to provide a fairly concise picture of both the prey diversity in the cod's diet, and of the relative importance of the different prey. With the pronounced climatic variation in this region a marked seasonal variation both in food bulk and prey choice was expected. Although Arntz (1974) and others have demonstrated differences in the food of cod between fairly close stations, this was not anticipated within the relatively small and seemingly uniform Balsfjord. Because of the contradictory opinions as to whether cod feed at spawning time or not (Love, 1970; Dambergs, 1964), we also wanted to find out how the Balsfjord cod behaved in this respect. Brunel (1965) and others have found that cod, although usually a demersal fish, may undertake prolonged excursions into midwater to feed. The analysis should therefore, include appraisal of such prey in the Balsfjord.

## Material and methods

The Balsfjord is situated at 69°N latitude. It is a silled fjord, 3 to 6 km wide, which meanders gently for about 60 km in a southeasterly direction from Tromsö. The sill area is a complex of several sounds and islands (Fig. 1). The maximum sill depth is 35 m and the maximum basin depth 195 m. The sides are steep and much of the fjord is deeper than 100 m. The water is comparatively cold, because it is fairly well closed off from the warmer coastal current. The hydrography of the fjord is treated in detail by Sælen (1950) and Eilertsen et al. (1981).

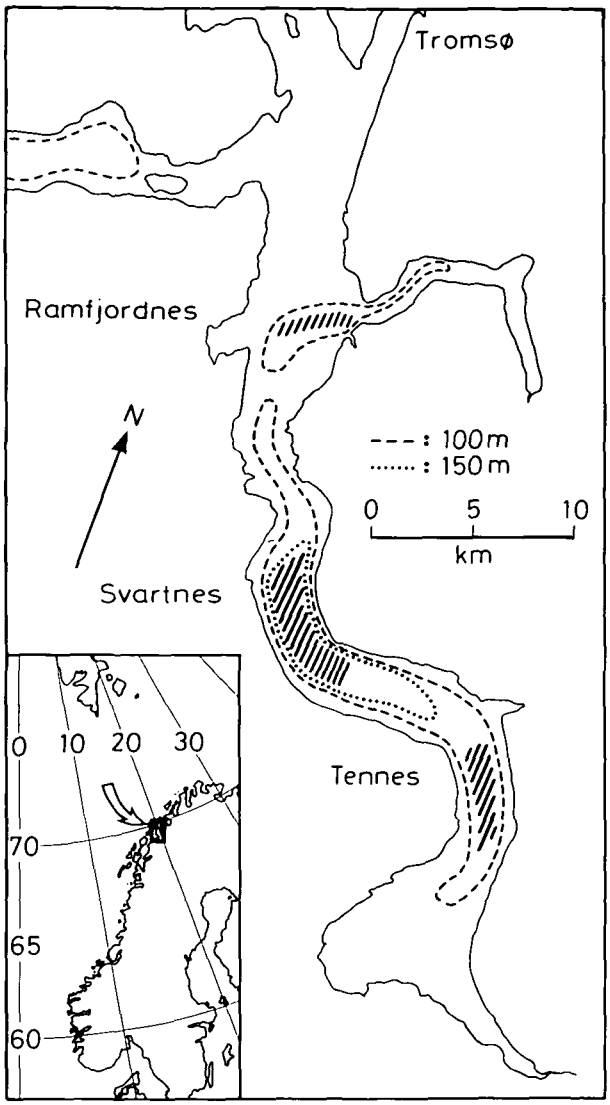


Figure 1. Chart of the Balsfjord. Prawn-trawling grounds used as sampling stations are hatched.

Fish sampling was confined to the soft-bottom, deepwater areas. These make up the largest part of the fjord, and previous experience indicated that the cod lived regularly there for most of the year. A one-year sampling programme was set up at three stations, with sampling intervals of 1 to 2 months.

The sampling stations, named after the closest point ashore, are shown in Figure 1. All three are prawn-trawling grounds. Svartnes is the largest and deepest area, at a fairly constant depth of 185 m. Tennes and Ramfjordnes are both smaller and shallower grounds with a depth range of 100 to 125 m. The Tennes station is situated close to two shallow bights at the end of the Balsfjord. The Ramfjordnes station borders the sill itself and is also close to the Ramfjord, a small side branch of the Balsfjord.

Table 1. The occurrence of herring, capelin, and prawns in the trawl and in the cod stomachs sampled from the same catch. The number of hauls is indicated.

| Combination | Prey | | |
|---|---|---|---|
| | Herring | Capelin | Prawn |
| Some, or much in stomach, nothing in trawl | 1 | 9 | 15 |
| Nothing in stomach, some, or much in trawl | 6 | 3 | – |
| Nothing, some, or much both in stomach and trawl | 27 | 22 | 19 |
| Number of hauls | 34 | 34 | 34 |

Fish were caught with a prawn otter trawl operated from the RV "Asterias". The ground rope at the mouth of the net was 35 m, and the stretched mesh size in the codend was 40 mm. Sampling started in February 1975 and was repeated monthly, except for July, October, and December, until January 1976. Trawling time per haul was one hour except at Ramfjordnes where the size of the field restricted the time to 45 minutes. At each station two separate hauls were taken in order to test the reproducibility of the sampling.

After analysis of the stomach content the duplicate samples at each station were compared. Differences were found in some pairs of hauls, but no more than could be expected from the stomach analyses of a polyphagous species. Other pairs were very similar. All duplicates were pooled into one sample which was accepted as representative for that station and time.

The three stations were always sampled during the day time on the same day or on two consecutive days. During these cruises a pelagic trawl was used at night to catch young capelin. On two occasions this trawl caught enough cod to provide a sample. These fish were included in the material for comparison with benthic cod.

On board the research vessel all cod were measured to total length, sexed, and the maturation of the gonads was determined according to a five-stage scheme. Stomachs were cut off at the pharynx and pylorus and preserved individually in ethanol. Inverted stomachs were omitted as they introduce a bias (Daan, 1973).

The stomachs were analysed using the points method of Hynes (1950) with some modifications. Each stomach was opened and its fullness was determined according to a scale allotting 100 points to a completely full stomach and zero points to an empty stomach. After identification each food item was given a number of points according to its relative contribution to the total stomach content. Empty stomachs were included in all calculations. Following Tyler (1972), the term *principal prey* was used for those food items that occurred in at least 5 % of the stomachs from any station.

Cod sizes ranged from 18·5 to 74 cm, but few were

Table 2. The number of fish caught in the prawn trawl at three stations in the Balsfjord from February 1975 to January 1976. Total trawling time 47·5 h.

| Species | Station | | | |
|---|---|---|---|---|
| | Ramfjordnes | Svartnes | Tennes | Total |
| Starry ray, *Raja radiata* | – | 4 | – | 4 |
| Herring, *Clupea harengus* | 263 | 39 | 759 | 1 061 |
| Sprat, *Clupea sprattus* | 14 | 16 | – | 30 |
| Capelin, *Mallotus villosus* | 25 | 842 | 245 | 1 112 |
| Sheppy argentine, *Maurolicus muelleri* | 1 | – | 1 | 2 |
| Norway pout, *Trisopterus esmarkii* | 7 | – | 2 | 9 |
| Whiting, *Merlangius merlangus* | – | – | 1 | 1 |
| Haddock, *Melanogrammus aeglefinus* | 5 | 1 | 1 | 7 |
| Cod, *Gadus morhua* | 612 | 313 | 512 | 1 437 |
| Snake blenny, *Lumpenus lumpretaeformis* | 9 | 12 | 43 | 64 |
| Redfish, *Sebastes* sp. | 2 | 2 | 3 | 7 |
| *Leptagonus decagonus* | – | – | 1 | 1 |
| Halibut, *Hippoglossus hippoglossus* | – | – | 1 | 1 |
| Long-rough dab, *Hippoglossoides platessoides* | 246 | 18 | 453 | 717 |
| Plaice, *Pleuronectes platessa* | 18 | – | – | 18 |
| Witch, *Glyptocephalus cynoglossus* | 2 | 1 | – | 3 |
| Total | 1 204 | 1 248 | 2 022 | 4 474 |

Table 3. Frequency of occurrence of all identified taxa in the stomachs of cod at three stations in the Balsfjord from February 1975 to January 1976.

| Taxon identified | Station | | | | | |
|---|---|---|---|---|---|---|
| | Ramfjordnes | | Svartnes | | Tennes | |
| | *n* | % | *n* | % | *n* | % |
| Anthozoa | | | | | | |
| *Hormatia* sp. | – | – | 1 | 0·5 | 7 | 2·1 |
| Polychaeta errantia | | | | | | |
| *Aphrodita aculeata* | – | – | – | – | 1 | 0·3 |
| *Harmothoe sarsi* | – | – | 1 | 0·5 | 1 | 0·3 |
| Aphroditidae | – | – | – | – | 1 | 0·3 |
| *Nephtys* sp. | 65 | 13·2 | 7 | 3·2 | 51 | 15·3 |
| *Lumbrinereis* sp. | 1 | 0·2 | – | – | 3 | 0·9 |
| *Eunice pennata* | 1 | 0·2 | – | – | – | – |
| Polychaeta sedentaria | | | | | | |
| *Flabelligera affinis* | 1 | 0·2 | – | – | – | – |
| *Brada* sp. | – | – | – | – | 1 | 0·3 |
| *Maldane sarsi* | – | – | 1 | 0·5 | 1 | 0·3 |
| Maldanidae | 2 | 0·4 | – | – | 4 | 1·2 |
| *Pectinaria* sp. | 3 | 0·6 | 1 | 0·5 | 1 | 0·3 |
| *Terebellides stroemii* | 1 | 0·2 | – | – | 1 | 0·3 |
| Terebellidae | 1 | 0·2 | – | – | – | – |
| Polychaeta | 8 | 1·6 | – | – | 5 | 1·5 |
| Gastropoda | | | | | | |
| Buccinidae | 1 | 0·2 | – | – | – | – |
| Opisthobranchia | 1 | 0·2 | – | – | 1 | 0·3 |
| Bivalvia | | | | | | |
| *Nucula tenuis* | – | – | – | – | 1 | 0·3 |
| *Yoldiella* sp. | 6 | 1·2 | 4 | 1·8 | 5 | 1·5 |
| *Chlamys* sp. | 1 | 0·2 | 1 | 0·5 | – | – |
| *Thyasira* sp. | – | – | – | – | 1 | 0·3 |
| Bivalvia | – | – | – | – | 1 | 0·3 |
| Cephalopoda | | | | | | |
| *Todarodes sagittatus* | – | – | 1 | 0·5 | – | – |
| Copepoda | | | | | | |
| *Calanus finmarchicus* | 6 | 1·2 | 1 | 0·5 | – | – |
| *C. hyperboreus* | 1 | 0·2 | – | – | – | – |
| *Metridia longa* | 3 | 0·6 | – | – | – | – |
| Copepoda | 4 | 0·8 | – | – | 2 | 0·6 |

Contd

Table 3 contd

| Taxon identified | Station Ramfjordnes | | Svartnes | | Tennes | |
|---|---|---|---|---|---|---|
| | *n* | % | *n* | % | *n* | % |
| Mysidacea | | | | | | |
| *Erythrops* sp. | 31 | 6·3 | 20 | 9·0 | 42 | 12·6 |
| *Pseudomma truncatum* | 8 | 1·6 | 2 | 0·9 | 4 | 1·2 |
| *Michteimysis mixta* | 20 | 4·1 | 35 | 15·8 | 35 | 10·5 |
| Mysidacea | 5 | 1·0 | 7 | 3·2 | 3 | 0·9 |
| Isopoda | | | | | | |
| *Idothea granulosa* | 1 | 0·2 | – | – | – | – |
| *Munnopsis typica* | 6 | 1·2 | 8 | 3·6 | 1 | 0·3 |
| Isopoda | 2 | 0·4 | 2 | 0·9 | 4 | 1·2 |
| Amphipoda | | | | | | |
| *Parathemisto abyssorum* | 12 | 2·4 | 3 | 1·4 | 15 | 4·5 |
| *Stegocephalus inflatus* | – | – | – | – | 1 | 0·3 |
| *Ampelisca* sp. | 3 | 0·6 | – | – | 1 | 0·3 |
| *Liljeborgia fissicornis* | – | – | – | – | 1 | 0·3 |
| *Paroediceros lynceus* | 1 | 0·2 | – | – | – | – |
| *Arrhis phyllonyx* | 19 | 3·9 | – | – | 37 | 11·0 |
| *Halirages fulvocinctus* | 7 | 1·4 | 18 | 8·1 | 9 | 2·7 |
| *Rhachotropis macropus* | 2 | 0·4 | 20 | 9·0 | 10 | 3·0 |
| *Gammarus locusta* | 1 | 0·2 | – | – | – | – |
| *Gammarellus homari* | 1 | 0·2 | – | – | – | – |
| *Moera loveni* | 3 | 0·6 | 1 | 0·5 | 1 | 0·3 |
| *Melita formosa* | – | – | – | – | 1 | 0·3 |
| *Caprella* sp. | 2 | 0·4 | – | – | 1 | 0·3 |
| Amphipoda | 13 | 2·6 | 10 | 4·5 | 6 | 1·8 |
| Euphausiacea | | | | | | |
| *Meganyctiphanes norvegica* | 10 | 2·0 | 48 | 21·6 | 6 | 1·8 |
| *Thysanoessa inermis* | 22 | 4·5 | 23 | 10·4 | 27 | 8·1 |
| *T. raschii* | 37 | 7·5 | 15 | 6·8 | 30 | 9·0 |
| *Thysanoessa* spp. | 147 | 29·8 | 51 | 23·0 | 45 | 13·5 |
| Decapoda natantia | | | | | | |
| *Spirontocaris liljeborgii* | – | – | 1 | 0·5 | – | – |
| *Lebbeus polaris* | 1 | 0·2 | – | – | – | – |
| *Eualus gaimardii* | 1 | 0·2 | – | – | – | – |
| *Pandalus borealis* | 125 | 25·3 | 104 | 46·8 | 112 | 33·5 |
| *Pandalus montagui* | – | – | – | – | 1 | 0·3 |
| *Sabinea sarsii* | 1 | 0·2 | 1 | 0·5 | 1 | 0·3 |
| *S. septemcarinatus* | 6 | 1·2 | 4 | 1·8 | 4 | 1·2 |
| *Sabinea* spp. | 1 | 0·2 | – | – | 1 | 0·3 |
| Decapoda reptantia | | | | | | |
| *Hyas araneus* | 3 | 0·6 | – | – | 2 | 0·6 |
| *H. coarctatus* | 2 | 0·4 | – | – | 1 | 0·3 |
| *Pagurus* sp. | 1 | 0·2 | 1 | 0·5 | 2 | 0·6 |
| Chaetognatha | | | | | | |
| Chaetognatha | 11 | 2·2 | 1 | 0·5 | 18 | 5·4 |
| Echinodermata | | | | | | |
| *Astropecten irregularis* | 1 | 0·2 | 2 | 0·9 | – | – |
| *Ophiura sarsii* | 1 | 0·2 | – | – | – | – |
| Ophiuroidea | – | – | 1 | 0·5 | – | – |
| Holothuroidea | 5 | 1·0 | 1 | 0·5 | 4 | 1·2 |
| Pisces | | | | | | |
| Hypotremata (ova) | – | – | – | – | 1 | 0·3 |
| *Clupea harengus* | 23 | 4·7 | 5 | 2·3 | 49 | 14·7 |
| *C. sprattus* | – | – | – | – | 1 | 0·3 |
| *Mallotus villosus* | 44 | 8·9 | 109 | 49·1 | 40 | 12·0 |
| *Merlangius merlangus* | 1 | 0·2 | – | – | – | – |
| *Gadus morhua* | 5 | 1·0 | – | – | 1 | 0·3 |
| *Brosme brosme* | – | – | 1 | 0·5 | – | – |
| *Ammodytes tobianus* | 1 | 0·2 | – | – | – | – |
| *Pholis gunnellus* | 1 | 0·2 | – | – | 1 | 0·3 |
| *Lumpenus lumpretaeformis* | 3 | 0·6 | 2 | 0·9 | 18 | 5·4 |
| *Leptoclinus maculatus* | 5 | 1·0 | – | – | 1 | 0·3 |
| *Sebastes* sp. | – | – | – | – | 1 | 0·3 |
| *Hippoglossoides platessoides* | 6 | 1·2 | 1 | 0·5 | 3 | 0·9 |
| Pisces | 23 | 4·6 | 4 | 1·8 | 17 | 5·1 |

below 25 or above 65 cm. The size distribution within the samples was fairly constant. The percentage distribution of the three length classes, below 35 cm, 35 to 55 cm, and above 55 cm, was usually about 15 %, 70 %, and 15 %: middle-sized fish always dominated. Since the small sample sizes did not allow splitting into size classes, the analysis was made under the assumption that the samples were comparable with respect to fish size.

A total of 1089 stomachs was analysed. Of these 39 were from fish caught in midwater. Sample size varied from five to 87 stomachs.

The possibility of introducing a bias to food analysis by using the trawl as sampling gear has been raised by Brown and Cheng (1946) and others. It is claimed that cod may eat prawns, small fish, or other food items which are concentrated in the net during towing. This possibility was tested on the present material by comparing the occurrence and abundance of prawns, capelin, and herring in the trawl catches and in the cod stomachs taken from the same hauls (Table 1). There were many cases when the prey occurred in the stomachs but not in the net or vice versa. This strongly justifies rejection of the hypothesis that the cod were feeding in the net. On the other hand there were also many cases when there was a good correlation between the trawl catch and stomach contents of the cod. However, these cases are inconclusive because they may well reflect situations when the abundance of the prey species at the sea floor is represented in the same way both in the trawl and in the cod stomachs. It was concluded that trawl sampling did not bias the results in the present study.

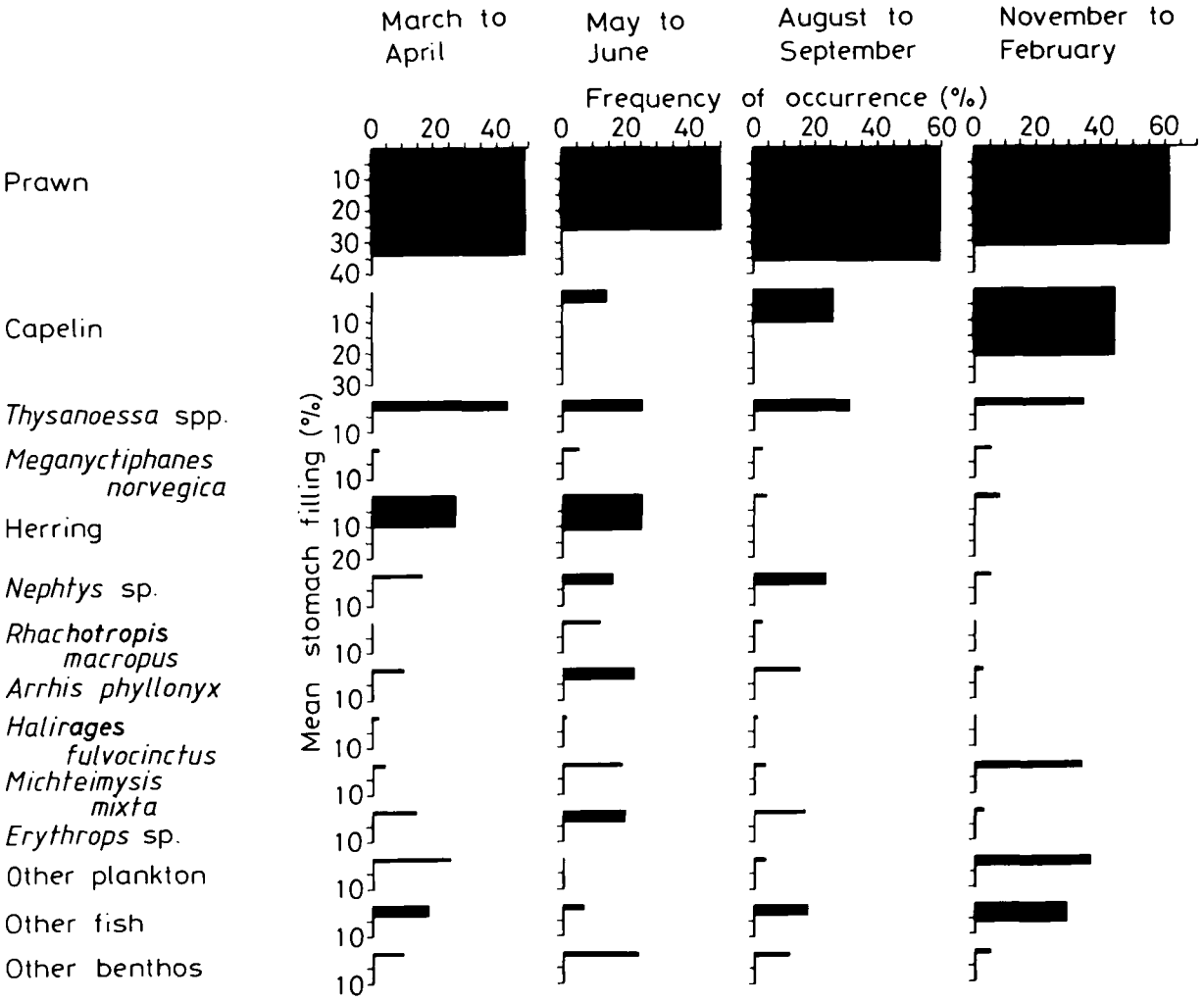


Figure 2 a. Tennes station. Seasonal variation of food items in the stomach contents. The importance of each prey or prey group is given in terms of its frequency of occurrence (%) in and mean contribution to the stomach contents (%).

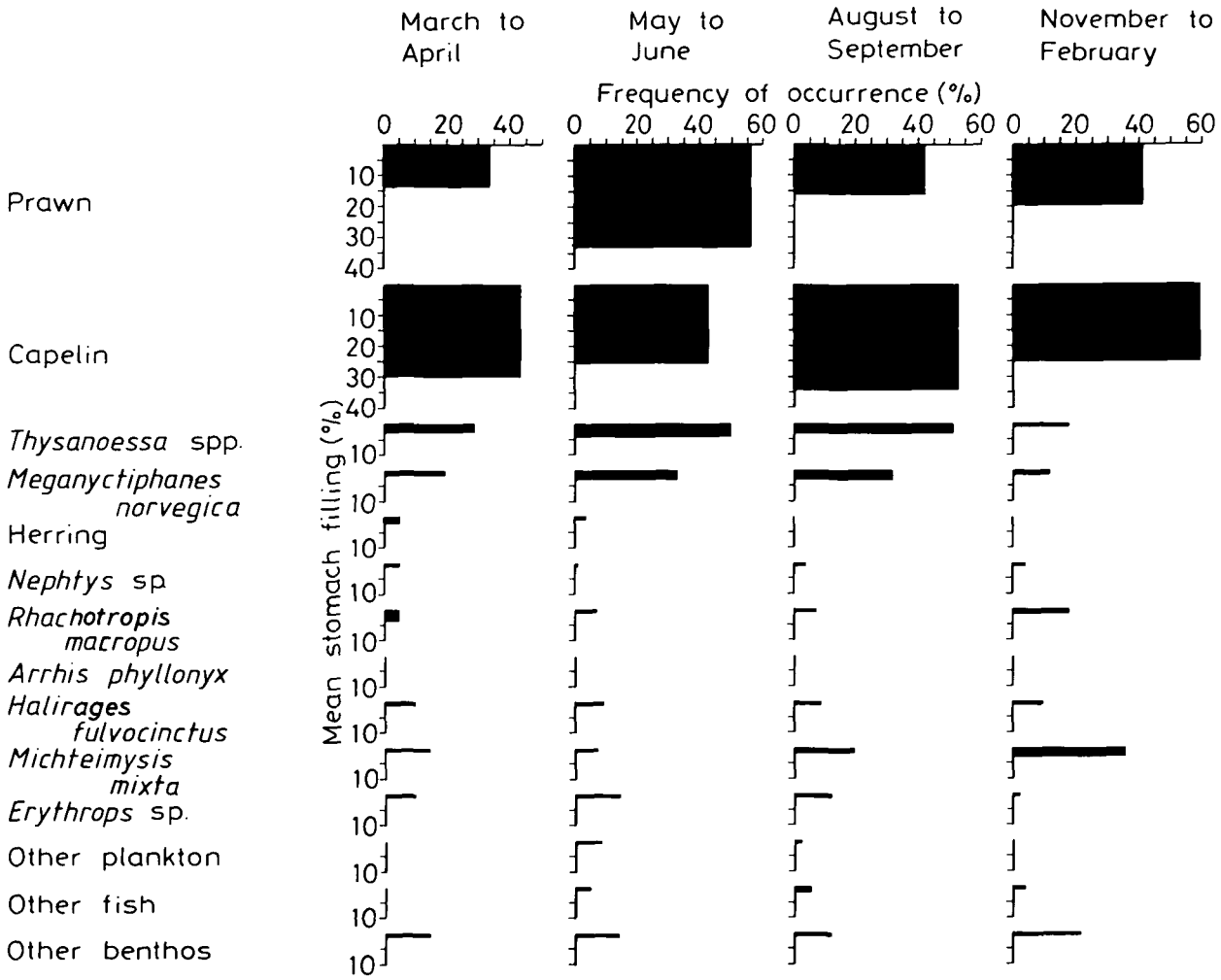


Figure 2 b. Svartnes station. Seasonal variation of food items in the stomach. The importance of each prey or prey group is given in terms of its frequency of occurrence (%) in and mean contribution to the stomach contents (%).

## Results

During the sampling period (Table 2) 16 species of fish were recorded. Capelin, cod, herring, and long-rough dab numerically made up 97 % of the total catch. Cod were abundant at all stations. Herring and dab were rare at Svartnes and capelin at Ramfjordnes. The diversity of fish species was slightly lower at Svartnes than at the other two stations.

The food spectrum of cod was considerable (Table 3), 72 different taxa being recorded. Of these, 54 occurred at Ramfjordnes and 51 at Tennes, while only 34 were found in the Svartnes material. The tendency to a lower diversity at Svartnes was also apparent within most taxonomic groups (Table 3). Relatively few of the food items were important prey. Only 14 of the identified taxa occurred in more than 5 % of the stomachs at any station and two, the chaetognaths and the snake blenny, were clearly less common than the other 12. They were therefore omitted as principal prey. The two species of *Thysanoessa* were pooled for further treatment because often they could not be distinguished in the stomach contents. Thus only 11 taxa were designated as principal prey items. These comprised two species of fish (capelin and herring), one prawn (*Pandalus borealis*), two taxa of krill (*Meganyctiphanes norvegica* and *Thysanoessa* spp.), three amphipods (*Rhachotropis macropus, Arrhis phyllonyx,* and *Halirages fulvocinctus*), two mysids (*Michteimysis mixta* and *Erythrops* sp.) and one polychaete (*Nephtys* sp., mainly *Nephtys ciliata*).

*P. borealis,* capelin, and krill, in that order, were the main food items of the Balsfjord cod (Fig. 2 a–c). With respect to quantity, or frequency of occurrence, or both, these three items stood out among the principal prey. Their relative importance as well as that of the other main items differed, however, at the three stations in the fjord.

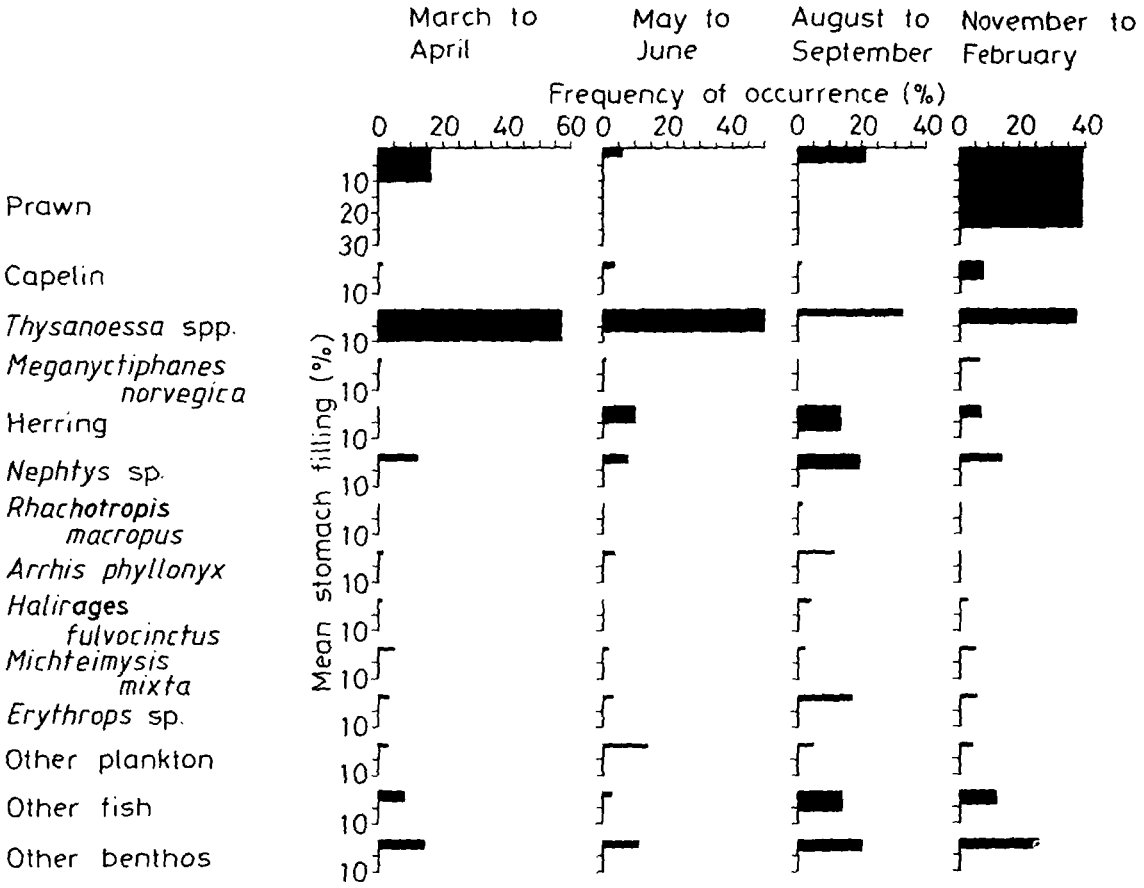


Figure 2 c. Ramfjordnes station. Seasonal variation of food items in the stomach contents. The importance of each prey or prey group is given in terms of its frequency of occurrence (%) in and mean contribution to the stomach contents (%).

*P. borealis* was the principal food at the Tennes station (Fig. 2 a), occurring in high frequencies and large quantities in all seasons. Capelin, on the other hand, was highly abundant and frequent only during the period November to February. From March to April this food item was absent. Small krill showed high frequencies of occurrence in all seasons, but the quantity was always comparatively low. Herring were quite important during the periods March to April and May to June, but not during the other sampling periods. *Nephtys* sp., *A. phyllonyx*, and the two mysids occurred in moderately high frequencies in two or three of the periods. The other principal prey items were not important (Fig. 2 a).

At Svartnes capelin were the predominant food of cod. The quantities and frequencies of this prey were always high at this station (Fig. 2 b). *P. borealis* also occurred in high frequencies, but in less quantities than capelin except in May to June (Fig. 2 b). Both large and small krill usually had high frequencies of occurrence, but the quantities were invariably low. Svartnes was the only station where *M. norvegica* was a common food item. The other principal prey had little importance, with the exception of *M. mixta* which were found in many stomachs during the period November to February. *A. phyllonyx* were totally absent from the cod stomachs at Svartnes.

The food of cod from Ramfjordnes was remarkable not only because capelin were unimportant, but also because of the comparatively small amount of prawns in the stomachs (Fig. 2 c). Small krill were always frequent, and generally the bulk of this food in the stomachs was somewhat higher here than at the other stations. In addition herring and *Nephtys* sp. showed some importance in the diet. The significance of the remaining principal prey items was small at Ramfjordnes, except for *Erythrops* sp. in August to September.

Stomachs with krill in substantial amounts (more than 25 points) contained significantly less other food items than those with considerable quantities of capelin or prawns. Comparisons between capelin-dominated and prawn-dominated stomachs failed to reveal any differences in this respect.

At all stations the fullness of the stomachs varied

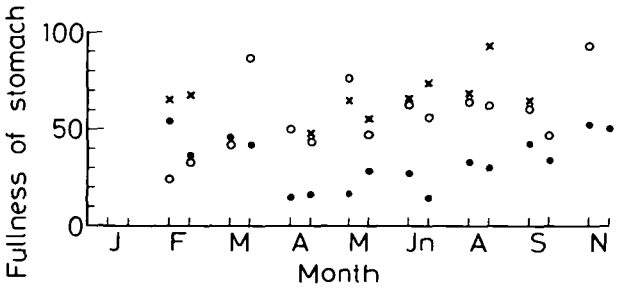


Figure 3. The fullness of cod stomachs in relation to season. Filled circles, Ramfjordnes station; crosses, Svartnes station; open circles, Tennes station.

Table 4. The number of stomachs in different ranges of fullness for unripe and ripening cod in March 1975. The hypothesis of identical distribution of fullness could not be rejected. For the $G$-test, $G = 0{\cdot}676 < \chi^2_{0{\cdot}05,2} = 5{\cdot}991$.

| Degree of maturation | Ranges of fullness, points 0–5 | 6–75 | 76–100 |
|---|---|---|---|
| Unripe (stage 0–I) | 25 | 25 | 27 |
| Ripening (stage II–III) | 12 | 15 | 19 |

Table 5. The number of stomachs in different ranges of fullness for non-spawning, spawning, and spent cod in April and May 1975. The hypothesis that stomach fullness was independent of degree of maturation could not be rejected. For the $G$-test, $G = 2{\cdot}43 < \chi^2_{0{\cdot}05,4} = 9{\cdot}488$.

| Degree of maturation | Ranges of fullness, points 0–5 | 6–75 | 76–100 |
|---|---|---|---|
| Non-spawning (stage 0–III) | 30 | 31 | 24 |
| Spawning (stage IV) | 37 | 25 | 21 |
| Spent (stage V) | 21 | 24 | 15 |

from month to month without any seasonal trends (Fig. 3). It also varied consistently between the stations. Cod from Ramfjordnes usually had less food in their stomachs than those from Svartnes while those from Tennes occupied the intermediate position.

The bulk of food in the stomachs of fish that were about to spawn was not significantly different from that of fish with undeveloped gonads (Table 4). Neither could any differences be observed in this respect between fish that were actually spawning, newly spent, or not spawning (Table 5).

The two samples of cod caught by pelagic trawl were strikingly different (Table 6). The Tennes sample had chiefly fish and benthos in the stomachs which were not very full. The prey composition was very similar to that of the bottom-trawl sample from the same station at the same time, and also to that of the bottom-trawl sample taken concurrently with the other pelagic sample. The Svartnes pelagic sample was totally dominated by small krill, *Thysanoessa* spp., and the stomachs were very full. The prey composition differed very much both from that of the Tennes sample and that of the concurrent bottom-trawl sample taken at Svartnes (Table 6).

## Discussion

All comprehensive studies on the food of cod have shown that a wide variety of prey species is taken; usually between 50 and 150 different taxa have been reported. On the other hand comparatively few species, up to about 15, are important elements in the diet (see Powles, 1958; Popova, 1963; Kohler and Fitzgerald, 1969; Tyler, 1972; Bowman, 1975 for the West Atlantic; Meschkat, 1936 for Iceland; Rae, 1967 a, b; 1968 for Iceland, Faroes and Scotland; Daan, 1973 for the North Sea; Chrzan, 1962; Strzyzewska, 1962; Arntz, 1971, 1974, for the Baltic; Denstadli, 1972 for the

Table 6. Stomach contents of cod from two pelagic trawl hauls and the bottom-trawl hauls on the same date and from the same station. The figures refer to the stomach fullness F, and the frequency of occurrence of prey, O (%).

| Prey | Tennes, March | | | | Svartnes, April | | | |
|---|---|---|---|---|---|---|---|---|
| | Pelagic trawl | | Bottom trawl | | Pelagic trawl | | Bottom trawl | |
| | F | O | F | O | F | O | F | O |
| *P. borealis* | 10·1 | 16 | 22·3 | 41 | 1·0 | 5 | 23·7 | 50 |
| Capelin | 11·7 | 22 | 9·7 | 14 | 1·6 | 5 | 10·0 | 20 |
| *Thysanoessa* spp. | 0·2 | 16 | 0·3 | 9 | 57·4 | 100 | 1·6 | 30 |
| *M. norvegica* | – | – | – | – | – | – | 2·7 | 40 |
| Herring | – | – | 4·5 | 5 | – | – | 4·0 | 10 |
| *Nephtys* sp. | 2·4 | 39 | 4·6 | 18 | 0·5 | 5 | 0·5 | 10 |
| *A. phyllonyx* | 0·3 | 11 | 0·3 | 9 | – | – | – | – |
| *M. mixta* | 0·1 | 6 | 0·7 | 9 | – | – | – | – |
| Other fish | 4·1 | 28 | 9·3 | 18 | 0·5 | 5 | – | – |
| Other benthos | 1·8 | 11 | – | – | 3·1 | 14 | 2·5 | 20 |
| Number of fish | 18 | | 21 | | 22 | | 10 | |
| Mean fullness of stomachs | 30·7 | | 51·7 | | 64·1 | | 45·0 | |

Trondheimsfjord; Brown and Cheng, 1946; Zadulskaia and Smirnov, 1939; Zatsepin and Petrova, 1939 for the Barents Sea).

The present results for the Balsfjord cod fit well into this general picture (Table 3). Usually active and conspicuous, epibenthic, semipelagic, or pelagic species dominate the food of cod. Crustaceans and fish are almost always important elements in the diet. Polychaete worms may also be significant. On occasions ctenophores (Graham et al., 1954; Popova, 1963), molluscs (Arntz, 1973), echinoderms (Brown and Cheng, 1946), and ascidians (Denstadli, 1972) have been reported as important food. These tendencies were also reflected in the Balsfjord. Crustaceans and fish made up most of the principal prey, the epibenthic polychaete *Nephtys* sp. being the only exception (Fig. 2 a–c). True infaunal elements were scarce in the diet (Table 3).

On both sides of the Atlantic a wider variety among the important prey is indicated in the southern parts of the cod's distribution area (Rae, 1967 a; Tyler, 1972; Daan, 1973; Bowman, 1975) as opposed to the northern parts where the number of important prey species is usually less than five (Brown and Cheng, 1946; Powles, 1958; Popova, 1963; Sidorenko, 1963; Novikova, 1965; Rae, 1968). There is a tendency that the subarctic (*sensu* Dunbar, 1968) endpoint of this trend everywhere is characterized by small krill (*Thysanoessa* spp.) and capelin (Brown and Cheng, 1946; Sidorenko, 1963; Novikova, 1965; Rae, 1968). Again the results from the Balsfjord agreed with the general picture, as two of the three most important of the principal prey were *Thysanoessa* spp. and capelin.

Wiborg (1948, 1949) studied the food of 0-, 1-, and 2-group cod in a wide range of coastal and fjord localities in northern Norway, including the Balsfjord. The results cannot be directly compared with the present material because his material consisted predominantly of very small (0-group) fish. Nevertheless, it is interesting to note that *Thysanoessa inermis* were the dominant prey of the small cod and that several of the principal prey in the present study (*Erythrops* sp., *M. mixta, P. borealis, R. macropus,* and *H. fulvocinctus*) also were recorded as important in his material.

Pearcy et al. (1979) examined a relatively small number of cod stomachs from Svartnes and Tennes in the Balsfjord in the summer of 1978. Their principal aim was to compare the food of pelagic and demersal fish. For cod caught at the bottom their results agree reasonably well with the present data. The overall food diversity was considerably less, but there were no important discrepancies. Cod caught in midwater had predominantly eaten capelin and krill, but sometimes also a few prawns and other benthos. Pearcy et al. (1979) concluded that both capelin and krill were taken in the pelagic zone. The present results only partly confirm this. Krill are propably the only prey taken in midwater by the cod in the fjord. This is indicated by those stomachs which contained krill as the main food. They had less additional, mainly benthic, food than other stomachs. However, Evans and Hopkins (1981) have shown that sound-scattering layers attributed to krill often meet the bottom at daytime in north Norwegian fjords, which might give the cod an opportunity to feed upon krill along the bottom for some hours each day. The present results may be taken to indicate that this does not happen in the Balsfjord.

The capelin on the other hand is probably not taken in midwater. Stomachs with capelin as the main prey had as much additional, mainly benthic, food as stomachs with *P. borealis* as the main prey. This suggests that the capelin were usually taken near the bottom. Odd-Harald Johannessen (personal communication), who has sampled capelin extensively in the Balsfjord, states that it is chiefly a demersal fish. The trawling carried out in the present study confirmed this. Only the 0-group capelin lives exclusively in midwater, the older capelin probably spending most of its time near the bottom, where it is eaten by the cod.

Brown and Cheng (1946) and Arntz (1974) have shown that cod from fairly closely located sampling stations may eat quite different food. The three stations in the Balsfjord demonstrated this point clearly (Table 3, Fig. 2). The expectation that the cod had a similar diet at different places within the fjord could therefore not be confirmed. The diet at Tennes and Ramfjordnes appeared more varied than that at Svartnes (Table 3), which may be related to the size of the trawling grounds and also to their location in the fjord. Tennes and Ramfjordnes are small grounds and they have broad contact with larger and shallower areas (Fig. 1) with different prey communities. At both stations a pronounced edge effect is therefore likely. Moreover, the probability of catching fish that have fed in another area than the trawling ground is greater at these small stations than at Svartnes. The differences between Tennes and Ramfjordnes is probably caused by differences in the faunal elements at the end and the mouth of the fjord. The markedly lower food diversity of the cod caught at Svartnes (Table 3, Fig. 2) may be due to a lesser edge effect at this station because of its size (Fig. 1), but also to the less variable environmental conditions (light, temperature, substrate) at this large and deep trawling ground, (Sælen, 1950; Eilertsen et al. 1981).

The lack of seasonal trends in the degree of stomach filling (Fig. 3) shows that the extreme light regime at this latitude probably has little effect on the food intake of cod. Thus during the two months of polar darkness the cod had as much food in their stomachs as at other times of the year. Possibly tactile and gustatory receptors on barbels and pelvic fins are involved in prey location during dark periods (Brawn, 1969). Temperatures should not influence the feeding of deepwater cod in the Balsfjord because the seasonal variation is small below 100 m (Sælen, 1950; Eilertsen et al., 1981). Neither does spawning appear to affect food intake (Tables 4 and 5).

This is contradictory to the findings of most other authors. Ripe cod usually stop feeding around the spawning time (Rae, 1967 a; Chrzan, 1962; Denstadli, 1972; Arntz, 1973). Such a cessation of feeding combined with increasing energy demands of the growing gonads has been related to the protein depletion and high water content found in the North Sea cod muscle at spawning time (Ironside and Love, 1958; Love, 1970). In the Balsfjord, Eliassen (1978, and unpublished) found little protein depletion in the cod muscle prior to and during the spawning season. This agrees well with the present result that the Balsfjord cod does not stop feeding at spawning time. In Nova Scotia, Dambergs (1964) had results similar to those of Eliassen (1978), and he also stated that the cod there feed during the spawning season.

## Acknowledgements

Sincere thanks are due to the captain and crew of the "Asterias" Tormod Karlsen, Ola Lyngmo, Egil Johansen, Erling Pedersen, and Öystein Antonsen for their cooperation during the cruises; to Kai Myhr for the arduous job of sorting stomach material; to Eivind Oug and Wim Vader for help with the identification of some of the polychaetes and amphipods respectively; to Per Grotnes and Ola Vahl for commenting on the manuscript; and to Chris Hopkins for correcting the English.

## References

Arntz, W. E. 1971. A contribution to the feeding ecology of cod (*Gadus morhua* L.) in the western Baltic. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 166: 13–9.

Arntz, W. E. 1973. Periodicity of diel food intake of cod *Gadus morhua* in the Kiel Bay. Oikos (Suppl.), 15: 138–45.

Arntz, W. E. 1974. Die Nahrung juveniler Dorsche (*Gadus morhua* L.) in der Kieler Bucht. Ber. Deutsch. Wissenschaftl. Komm. Meeresforsch., 23: 97–120.

Bowman, R. E. 1975. Food habits of Atlantic cod, haddock, and silver hake in the Northwest Atlantic, 1969–1972. Nat. Mar. Fish. Serv., Northeast Fish. Center, Woods Hole, Lab. Ref., 75–1: 53 pp.

Brawn, V. M. 1969. Feeding behaviour of cod (*Gadus morhua*). J. Fish. Res. Bd Can., 26: 583–496.

Brown, W. W., & Cheng, C. 1946. Investigations into the food of the cod (*Gadus callarias* L.) off Bear Island, and of the cod and haddock (*G. aeglefinus* L.) off Iceland and the Murman coast. Hull Bull. Mar. Ecol., 3: 37–71.

Brunel, P. 1965. Food as a factor or indicator of vertical migrations of cod in the western Gulf of St. Lawrence. Spec. Publs int. Commn NW. Atlant. Fish., 6: 439–48.

Chrzan, F. 1962. The food and feeding of cod in the Gulf of Gdansk. Pr. morsk. Inst. ryb. Gdyni, 11/A: 161–99. (In Polish, English summary).

Denstadli, S. O. 1972. Forplantning, vekst og ernæring hos torsk (*Gadus morhua* L.) i Borgenfjorden, Nord-Tröndelag. Cand. real. thesis at the University of Trondheim, 111 pp. (In Norwegian, mimeo).

Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod, *Gadus morhua*. Neth. J. Sea Res., 6: 479–517.

Dambergs, N. 1964. Extractives of fish muscle. 4. Seasonal variations of fat, water-solubles, protein and water in cod (*Gadus morhua* L.) fillets. J. Fish. Res. Bd Can., 21: 703–9.

Dunbar, M. J. 1968. Ecological development in polar regions. A study in evolution. Prentice-Hall, Englewood Cliffs, N.J., 119 pp.

Eilertsen, H. C., Falk-Petersen, S., Hopkins, C. C. E., & Tande, K. 1981. Ecological investigations on the plankton community of Balsfjorden, northern Norway. The study area, topography and environmental parameters. Sarsia, 66: 25–34.

Eliassen, J. E. 1978. Årsvariasjon i vann, fett og protein i filét, lever og gonade hos torsk (*Gadus morhua* L.) fra Balsfjorden, Nord-Norge. Cand.real. thesis at the University of Tromsö, 127 pp. (In Norwegian, mimeo).

Eliassen, J. E. (unpublished). Seasonal variation of gonad size and protein and water content of cod *Gadus morhua* fillet from Balsfjorden, northern Norway.

Evans, R. A., & Hopkins, C. C. E. 1981. Distribution and standing stock of zooplankton sound-scattering layers along the north Norwegian coast in February–March, 1978. Sarsia, 66, 147–60.

Graham, M., Trout, G. C., Beverton, R. J. H., Corlett, J., Lee, A. J., & Blacker, R. W. 1954. Report on research from the "Ernest Holt" into the fishery near Bear Island 1949 and 1950. Fishery Invest., Lond., Ser. 2, 18(3): 87 pp.

Hynes, H. B. N. 1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. J. Anim. Ecol., 19: 36–58.

Ironside, J. I. M., & Love, R. M. 1958. Studies on protein denaturation in frozen fish. 1. – Biological factors influencing the amounts of soluble and insoluble protein in the muscle of the North Sea cod. J. Sci. Fd Agric., 9: 597–604.

Kohler, A. C., & Fitzgerald, D. N. 1969. Comparisons of food of cod and haddock in the Gulf of St. Lawrence and the Nova Scotia banks. J. Fish. Res. Bd Can., 26: 1273–87.

Love, R. M. 1970. The chemical biology of fishes. Acad. Press, London, New York. 547 pp.

Meschkat, A. 1936. Untersuchungen über den Aufbau der Kabeljaunahrung im Bereich der Vestmannainseln. Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer., 99: 1–19.

Novikova, N. S. 1965. Some problems concerning the food and feeding behaviour of cod and haddock in the Barents Sea. Trydy Murmansk. Biol. Inst., 7(11): 3–47. (Fish. Res. Bd Can. Transl. Ser., 774, 1966).

Pearcy, W. G., Hopkins, C. C. E., Grönvik, S., & Evans, R. A. 1979. Feeding habits of cod, capelin, and herring in Balsfjorden, northern Norway, July–August 1978: the importance of euphausiids. Sarsia, 64: 269–77.

Popova, O. A. 1963. Some data on the feeding of cod in the Newfoundland area of the northwest Atlantic. *In* Soviet fisheries investigations in the northwest Atlantic, pp. 228–48. Ed. by Y. Y. Marti. IPST 994, Jerusalem, 370 pp.

Powles, P. M. 1958. Studies of reproduction and feeding of Atlantic cod (*Gadus callarias* L.) in southwestern Gulf of St. Lawrence. J. Fish. Res. Bd Can., 15: 1383–1402.

Rae, B. B. 1967 a. The food of cod in the North Sea and on west of Scotland grounds. Mar. Res., 1967 (1): 68 pp.

Rae, B. B. 1967 b. The food of cod in Faroese grounds. Mar. Res., 1967 (6): 23 pp.

Rae, B. B. 1968. The food of cod in Icelandic waters. Mar. Res., 1968 (6): 19 pp.

Sidorenko, I. N. 1963. Feeding of cod in western Greenland waters. *In* Soviet fisheries investigations in the northwest Atlantic, pp. 249–55. Ed. by Y. Y. Marti. IPST 994, Jerusalem, 370 pp.

Strzyzewska, K. 1962. Nourishment and food of southern Baltic cod. Pr. morsk. Inst. ryb. Gdyni, 11/A: 387–419. (In Polish, English summary).

Sælen, O. H. 1950. The hydrography of some fjords in north Norway. Tromsö Mus. Årsh., 70: 1–93.

Tyler, A. V. 1972. Food resource division among northern, marine, demersal fishes. J. Fish. Res. Bd Can., 29: 997–1003.

Wiborg, K. F. 1948. Some observations on the food of cod (*Gadus callarias* L.) of the O–II-group from deep water and the littoral zone in northern Norway and from deep water at Spitzbergen. Fisk Dir. Skr., Serie Fiskeri Havundersøkelser, 9 (4): 19 pp.

Wiborg, K. F. 1949. The food of cod (*Gadus callarias* L.) of the O–II-group from deep water in some fjords of northern Norway. Fisk Dir. Skr., Serie Fiskeri Havundersøkelser, 9 (8): 27 pp.

Zadulskaia, E. S., & Smirnov, K. S. 1939. Diurnal pattern of feeding of cod on the fishing grounds of the Barents Sea. Trudy Vse. Nauko-Issled. Inst. Morsk. Rhyb. Khoz. Okeanogr., 4: 321–38. (Fish. Res. Bd Can. Transl. Ser., 483, 1964).

Zatsepin, V. J., & Petrova, N. S. 1939. The food of commercial stocks of cod in the southeastern part of the Barents Sea. Trudy pol. Inst. Morsk. Rhyb. Khoz. Okeanogr. (PINRO), 1939 (5): 1–700. (Fish. Res. Bd Can. Transl. Ser. 498, 1964).