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# Annual Variability in the Diet of Atlantic Cod (*Gadus morhua* L.) off Southern Labrador and Norhteast Newfoundland (Div. 2J+3K) in autumn, 1977-82

by

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## Abstract

Examination of the stomachs of 8800 Atlantic cod (*Gadus morhua*) collected off southern Labrador and northeast Newfoundland (NAFO Div. 2J+3K) during the autumns of 1977-82 revealed that the major prey were capelin (*Mallotus villosus*), shrimp (primarily *Pandalus borealis*), crabs (primarily *Chionoecetes opilio*), hyperiid amphipods and Arctic cod (*Boreogadus saida*). Predation on capelin was most intensive on Hamilton Bank and southward along the adjacent coastal shelf.

The rate of predation by Atlantic cod on capelin varied with capelin abundance. During the period of low capelin abundance in the late 1970's Atlantic cod did not compensate for reduced predation on capelin by preying more intensively on shrimp, crabs or other benthic invertebrates, but there was increased predation on Arctic cod and hyperiids. This increased predation on alternate prey only partially compensated for the reduction in predation on capelin.

Hyperiids may have been more abundant in the late 1970's, possibly as a result of decreased predation pressure from capelin.

## Introduction

Capelin (*Mallotus villosus*) is a major prey of Atlantic cod (*Gadus morhua*) off eastern Newfoundland and Labrador (Popova, 1962), at West Greenland (Hansen, 1949) and Iceland (Palsson, 1983), and in the Barents Sea (Grinkevich, 1957). The initiation of major fisheries for capelin in several of these areas has presented complex questions regarding management of a predatory-prey interaction. In the Newfoundland area exploitation rates for capelin have recently been set at the conservative level of 10%, partly in recognition of the importance of capelin to cod and other predators (Anon., 1982). The contribution of capelin to the diet of cod off eastern Newfoundland and Labrador has been estimated at about 30% (Campbell and Winters, 1973; Minet and Perodou, 1978), but the estimates are based on small data sets with limited spatial and seasonal sampling. The importance of capelin to the growth of cod was investigated by Akenhead *et al*. (1982), who could find no relationship between annual growth increments in cod and biomass of capelin off eastern Newfoundland and Labrador (NAFO Div. 2J+3K). Although Akenhead *et al*. (1982) expressed serious reservations concerning the appropriateness of the available data for addressing this question, they also pointed out that cod might not be strongly linked to capelin, and that other prey might provide adequate forage during periods of low capelin abundance.

There are many possible ways in which cod feeding might respond to changes in capelin abundance. Because capelin appears to be a preferred prey of cod, one might expect that as capelin abundance increases, the predation rate by cod would increase relatively rapidly at first and then more slowly, approaching a plateau (a "type 2" functional response). More complex relationships are possible (see, for example, the review by Begon and Mortimer (1981)). Thus, a small decline from maximum capelin abundance might result in a small decrease in the predation rate or in a large decrease, depending on the shape of the curve. Furthermore, the decrease in capelin consumption might result in a decrease of the same magnitude in total consumption, or might be compensated for, in whole or in part, by predation on other prey. These other prey could be (1) organisms which have not changed in abundance or (2) organisms which have increased in abundance as a consequence of the capelin decline because they are either competitors or prey of capelin.

An analysis of catch rates in the USSR autumn capelin fishery (Carscadden and Miller, MS 1982; Carscadden, MS 1983) and biomass estimates from USSR acoustic surveys (Bakanev, MS 1983) indicate that the abundance of capelin off eastern Newfoundland and Labrador (Div. 2J+3K) was high in the mid 1970's, declined to very low levels in the late 1970's, and increased again in the early 1980's. The purpose of this paper is to describe the prey spectrum and feeding intensity of cod in this area during the autumns of 1977-82, and to determine whether there has been annual variability in feeding associated with the dramatic changes in capelin abundance during this period.

## Materials and Methods

Stomachs were collected from Atlantic cod caught during stratified-random bottom-trawl surveys by the chartered research stern trawler Gadus Atlantica in NAFO Div. 2J+3K in autumn, 1977-1982 (Table 1). Stomachs were collected opportunistically in 1977. In 1978 a stratified-random sample of 5 fish per 10-cm length group was sampled from the catch of every set. In subsequent years the sample size was reduced to 3 per 10-cm length-group. Cod stomachs were individually tagged and preserved in a 1:10 formalin:sea water solution.

Examination involved separation of food items into taxonomic categories. Fish and decapod crustaceans were identified to species, but other groups were combined into higher order taxa (eg. Polychaeta, Euphausiacea). Items in each taxon were placed briefly on absorbent paper to remove excess liquid, and then weighed to the nearest 0.1 g. The relative quantity of food in the stomachs and the relative importance of individual prey types was assessed using three indices:

1) Percent occurrence (number of stomachs with specific prey as percentage of total number of stomachs).

2) Percent weight (total weight of specific prey in all stomachs as percentage of total weight of all prey) (gravimetric method).

3) Stomach fullness index:

Mean total fullness index (TFI) =

$$\frac{1}{n}\sum_{f=1}^{n}\frac{\text{weight of stomach contents of fish}_f}{(\text{length of fish}_f)^3}\times 10^4$$

where n is the number of stomachs examined.

Mean partial fullness index of $\text{prey}_p$ ($PFI_p$) =

$$\frac{1}{n}\sum_{f=1}^{n}\frac{\text{weight of prey}_p\text{ in fish}_f}{(\text{length of fish}_f)^3}\times 10^4.$$

The stomach fullness index can provide more insightful comparisons than the other methods. It is not strongly influenced by the frequent occurrence of small prey which contribute little to total weight, as is the occurrence method, and it is not strongly weighted by the infrequent occurrence of large prey in large predators, as is the gravimetric method.

## Results

### Prey spectrum

The prey spectrum of cod in 1982, the year with the most extensive sampling, was very broad, but only a few groups of organisms were important (Table 2). Fish were the major prey, contributing 67% by weight and 59% of the total fullness index. The dominant fish was capelin, Mallotus villosus, but flatfishes (F. Pleuronectidae) and eelpouts (F. Zoarcidae) were also important. A high proportion (31% by weight) of the fish was unidentified. The major invertebrates in terms of weight were shrimp, mainly Pandalus borealis, and crabs, mainly Chionoecetes opilio. Several invertebrate groups, such as polychaetes, gammarid and hyperiid amphipods, mysids and euphausiids, occurred frequently but were not important in terms of weight. The prey composition was very similar in other years but the relative importance of some of the groups varied, as will be discussed later.

The relative importance of the various prey varied with cod length (Fig. 1). Capelin was important for all but the smallest cod (<25 cm), with peak partial fullness indices in the

30-45 cm range. Flatfishes and eelpouts were consumed mainly by large cod (>75 cm). The pink shrimp (P. borealis) occurred in a wide size range of cod without any major peaks. Snow crab (C. opilio) were eaten by cod >35 cm and were most important in large cod (>65 cm). Hyperiid amphipods occurred in all but the largest cod (>80 cm). Gammarid amphipods were particularly important for small cod (<25 cm).

The total fullness index (TFI) peaked at 35-40 cm, declined in medium-sized cod (45-70 cm), and then increased in large cod (Fig. 1). This pattern also occurred in 1980 and 1981 (Fig. 2), but the curves were not as smooth as in 1982, probably because sample sizes were smaller in the two earlier years (Table 1). The peak at 35-40 cm corresponds to a peak in predation on capelin, and the rise of TFI in large cod reflects predation on flatfish and eelpouts (Fig. 1).

The cod which might be most affected by changes in capelin abundance are those within the length range for which capelin is the most important prey. This length range appears to be roughly 30-69 cm. Smaller cod prey primarily on various invertebrates, especially gammarid amphipods, and larger cod prey on larger fish and crabs in addition to capelin (Fig. 1). Subsequent analysis of spatial and annual variability is restricted to cod within the 30-69 cm length-range.

Spatial variability

Coarse spatial variability in predation on capelin was examined by plotting the mean PFI for capelin in all stomachs collected in 1981 from cod (30-69 cm) caught in each 0.5° latitude x 1.0° longitude area (Fig. 3). Predation on capelin was most intense on Hamilton Bank, but capelin were also found in cod on Harrison Bank to the northwest of Hamilton Bank, along the coastal shelf off southern Labrador and northeast Newfoundland and on Funk Island Bank. The variation in TFI (Fig. 4) was largely a reflection of the capelin distribution. Similar patterns in TFI and PFI for capelin were observed in 1980 and 1982.

Annual variability

Intensity of predation on various major prey may be compared for the years 1978 and 1980-82. The years 1977 and 1979 are not included because sample sizes were relatively small. In addition, most sampling in 1977 was in Div. 2J and sampling in 1979 was earlier in the autumn than most sampling in other years (Table 1).

The PFI for capelin increased from a very low level in 1978 to a peak in 1981 and declined in 1982 (Table 3). Arctic cod (Boreogadus saida) were present but not important. Many prey were identified as Gadidae. Almost all of these were of the same size as Arctic cod found in the stomachs and caught by the trawl. Since very few Atlantic cod of comparable size were taken by the trawl, it may be assumed that most prey identified as Gadidae were Arctic cod. Gadidae and Arctic cod combined were more important than capelin in 1978 and 1980, but the PFI values in those years were much lower than those of capelin in 1981 and 1982. Other fish prey combined were relatively unimportant and did not vary greatly. Shrimp and crabs tended to remain fairly constant through the period, although Chionoecetes opilio did show a small but consistent increase from 1978 to 1982. Hyperiid amphipods declined from 0.31 in 1978 to 0.05 in 1982.

The total fullness index increased from 0.93 in 1978 to 1.18 in 1980 and 1.76 in 1981, and then declined to 1.13 in 1982. The peak in 1981 is clearly attributable to a peak in feeding on capelin. The TFI is higher in 1980 than in 1982, despite less predation on capelin, partly because of greater predation on Arctic cod and hyperiid amphipods. Annual comparisons are confounded by the high and variable quantities of unidentified fish and unidentified material.

A similar comparison among years may be made for Hamilton Bank alone, where predation on capelin was most intense (Fig. 3) and the influence of variability in capelin abundance may be most pronounced. For this study, Hamilton Bank is defined as the area bounded by 53°00'N, 56°10'W, 55°20'N (the 2J-2H boundary), and the 400 m isobath. The patterns seen in 2J+3K as a whole (Table 3) are also evident on Hamilton Bank (Table 4). However, the partial fullness indices for both capelin and Arctic cod are much higher in any given year on Hamilton Bank than in 2J+3K as a whole, and the total fullness index varies by a factor of 3 rather than a factor of 2.

The data for Hamilton Bank in 1977 and 1979 are not comparable to 1978 and 1980-82 because sample sizes are smaller and cod were not sampled from large areas of the bank. However, there were interesting features worth noting (Table 4). In 1977 there was considerable predation on juvenile (<10 cm) Greenland halibut (Reinhardtius hippoglossoides), and in 1979 there was intensive predation on hyperiid amphipods. In addition, predation on capelin was very low in both years.

## Discussion

The major prey of Atlantic cod off southern Labrador and northeastern Newfoundland during the autumns of 1980-82 was capelin. This is in agreement with Turuk (1968), who found during her studies in 1966-68 that capelin was the major prey of cod from July to December. Capelin were particularly abundant on Hamilton Bank and southward along the adjacent coastal shelf (Fig. 3), which is where highest concentrations were found during hydroacoustic surveys by the USSR (Bakanev, MS 1981, MS 1983) and Canada (J. Carscadden, Department of Fisheries and Oceans, St. John's, Nfld., pers. comm.). Popova (1962) found during the summer of 1960 that the proportion of cod feeding on capelin was higher near the coastal shelf than near the continental slope, although in August 1959, cod near the northeast edge of Belle Isle Bank were feeding very intensively on capelin.

The intensity of predation on capelin varied greatly among years, especially on Hamilton Bank. Quantitative comparisons between recent year and the 1960's (Popova, 1962; Turuk, 1968) are not possible because most of the earlier observations were reported as percent occurrence, which can be misleading, and the specific areas sampled were not stated. The variations in 1978-82 are similar to the changes in capelin biomass identified by hydroacoustic surveys (Bakanev, MS 1983) and by analysis of USSR catch and effort data (Carscadden and Miller, MS 1982; Carscadden, MS 1983). A direct comparison between predation rate and capelin abundance is not possible because the catch rate for 1980 is considered to be an unreliable indicator of stock abundance (Anon., 1981) and there was no hydroacoustic survey by the USSR in 1981 (Bakanev, MS 1983). It is nevertheless clear that when capelin are abundant they are the major prey of cod, and that in times of low capelin abundance the total quantity of food consumed is lower. That is, there appears to be no alternate prey which can completely replace capelin in the diet of cod in Div. 2J+3K in autumn.

Other prey of importance to cod are shrimp (mainly Pandalus borealis), crabs (mainly Chionoecetes opilio), hyperiid amphipods, and Arctic cod. Gammarid amphipods are major prey of small cod and flatfish and eelpouts are important for large cod. Only two of these prey, hyperiid amphipods and Arctic cod, were consumed to a greater extent during the period of reduced capelin abundance. Both are pelagic and could conceivably have benefited from reduced capelin abundance.

Hyperiids are a major prey of capelin in Div. 2J (Chan and Carscadden, MS 1976), and it is possible that their abundance increased under reduced predation pressure from capelin in the late 1970's and then declined as capelin abundance increased in the early 1980's. To my knowledge, there are no independent estimates of hyperiid abundance which can help test this hypothesis.

Arctic cod is a planktivore which, like capelin, feeds largely on calanoid copepods and hyperiids (Lilly, MS 1980). It is possible that Arctic cod were more successful when capelin abundance was low, and that the greater predation by Atlantic cod on Arctic cod during 1978 and 1980 compared with 1981-82 may reflect a higher absolute abundance of Arctic cod in the earlier years. However, the greater predation in 1978 and 1980 may simply reflect the high relative abundance of Arctic cod in the pelagic fish community noted during acoustic surveys by Canada in 1978, 1979, and 1980 (Miller, MS 1979; Carscadden and Miller, MS 1980; Miller and Carscadden, MS 1981) and by the USSR in 1978 and 1980 (Seliverstov and Serebrov, MS 1979; Bakanev, MS 1981). The commercial capelin fishery took a high by-catch of Arctic cod in 1979 (Maxim, MS 1980). The high relative abundance of Arctic cod in 1978-80 could have resulted from a severe reduction in capelin abundance with no absolute increase in Arctic cod abundance. The intensity of predation by Atlantic cod on Arctic cod in 1978 and 1980 was much lower than the intensity of predation on capelin in years of high capelin abundance (1981, 82). Arctic cod are not mentioned in reports of cod stomach examinations in this area during the 1960's (Popova, 1962; Turuk, 1968; Templeman, 1965; Templeman and May, 1965; Stanek, 1973) and the mid-1970's (Minet and Perodou, 1978).

Several tentative conclusions may be drawn from this short time-series of cod stomach examinations in Div. 2J+3K in autumn. (1) The feeding rate of cod on capelin depends on capelin abundance. (2) The total rate of food consumption by cod depends on capelin abundance. (3) In times of low capelin abundance cod do not feed much more intensively on benthic invertebrates, such as shrimp and crabs. (4) However, during periods of low capelin abundance a major prey of capelin, hyperiid amphipods in this case, may increase in abundance and be preyed on to a greater extent by cod. If this does occur, it is similar to the stabilizing effect of triangular food webs described by Ursin (1982), although in this case there is only partial replacement of capelin by hyperiids in the diet of cod.

A continuation of this time-series of cod stomach examinations may provide important insight into the feeding behaviour of cod at different levels of capelin abundance and into the response of an ecosystem to changes in abundance of a numerically important component.

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Table 1. Dates and samples sizes of stomach samples of Atlantic cod collected during stratified-random surveys by the Gadus Atlantica in NAFO Div. 2J+3K in autumn 1977-82.

| Year | Trip number | Sampling period | NAFO Div. | No. of[a] tows | No. of stomachs |
|---|---|---|---|---|---|
| 1977 | 3 | Nov. 11-Dec. 2 | 2J | 43 | 392 |
| | | | 3K | 5 | 72 |
| | | | | 48 | 464 |
| 1978 | 15 | Nov. 11-27 | 2J | 26 | 346 |
| | | | 3K | 46 | 693 |
| | | | | 72 | 1039 |
| 1979 | 27 | Sept. 29-Oct. 13 | 2J | 28 | 252 |
| | | | 3K | 35 | 292 |
| | | | | 63 | 544 |
| 1980 | 42 | Oct. 4-18 | 2J | 26 | 174 |
| | | | 3K | 44 | 334 |
| | 44 | Nov. 22-Dec. 8 | 2J | 52 | 756 |
| | | | 3K | 72 | 1059 |
| | | | | 194 | 2323 |
| 1981 | 58 | Nov. 15-29 | 2J | 76 | 786 |
| | | | 3K | 7 | 54 |
| | 59 | Dec. 3-13 | 3K | 56 | 564 |
| | | | | 139 | 1404 |
| 1982 | 71 | Oct. 30-Nov. 15 | 2J | 127 | 1706 |
| | | | 3K | 12 | 121 |
| | 72 | Nov. 20-Dec. 8 | 3K | 99 | 1227 |
| | | | | 238 | 3054 |
| Total 1977-82 2J+3K | | | | 754 | 8828 |

[a]Number of tows from which at least one stomach was collected.

Table 2. The food of Atlantic cod in NAFO Div. 2J+3K in autumn, 1982.

| | Percent[a] occurrence | Percent by weight | Mean[b] PFI |
|---|---|---|---|
| Invertebrata (misc.) | | 0.5 | 0.01 |
| Anthozoa | 4.9 | 1.0 | 0.01 |
| Ctenophora | 5.1 | 1.2 | 0.01 |
| Gastropoda | 4.3 | 0.3 | + |
| Cephalopoda | 3.7 | 0.4 | 0.01 |
| Polychaeta | 28.8 | 0.9 | 0.03 |
| Ophiuroidea | 2.1 | 0.1 | + |
| Crustacea | | | |
| Hyperiidae | 29.1 | 1.7 | 0.04 |
| Gammaridea | 43.3 | 0.8 | 0.04 |
| Mysidacea | 22.8 | 0.2 | 0.01 |
| Euphausiacea | 10.6 | 0.2 | 0.01 |
| Natantia | | | |
| *Pandalus borealis* | 24.4 | 4.8 | 0.08 |
| *Pandalus montagui* | 3.4 | 0.5 | 0.01 |
| Others and unid. | | 3.9 | 0.08 |
| Reptantia | | | |
| *Chionoecetes opilio* | 15.3 | 8.4 | 0.08 |
| *Hyas coarctatus* | 3.2 | 1.4 | 0.01 |
| Others and unid. | | 0.9 | 0.01 |
| Others and unid. | | 0.4 | 0.01 |
| Pisces | | | |
| *Mallotus villosus* | 9.9 | 16.0 | 0.28 |
| *Boreogadus saida* | 0.7 | 0.3 | + |
| Zoarcidae | | 5.8 | 0.03 |
| *Sebastes* sp. | 2.8 | 2.2 | 0.02 |
| Pleuronectidae | | 16.3 | 0.09 |
| Others | | 5.4 | 0.03 |
| Unidentified | | 21.0 | 0.30 |
| Unidentified and misc. | | 5.8 | 0.09 |
| Total | | | 1.27 |
| No. of stomachs 3077 | | | |
| Percent empty 2.7 | | | |

[a] Provided only for those taxa not initially identified at a lower taxonomic level.

[b] + indicates presence but PFI <0.005.

Table 3. Food of Atlantic cod (30-69 cm) in NAFO Div. 2J+3K in autumn, 1978 and 1980-82. Values are mean partial fullness indices.

| | 1978 | 1980 | 1981 | 1982 |
|---|---|---|---|---|
| Invertebrata (misc.) | 0.06 | 0.07 | 0.05 | 0.07 |
| Crustacea | | | | |
| Hyperiidae | 0.31 | 0.18 | 0.17 | 0.05 |
| Natantia | | | | |
| *Pandalus borealis* | 0.06 | 0.07 | 0.06 | 0.07 |
| Others and unid. | 0.12 | 0.11 | 0.10 | 0.09 |
| Reptantia | | | | |
| *Chionoecetes opilio* | 0.01 | 0.03 | 0.04 | 0.05 |
| Others and unid. | 0.02 | 0.02 | 0.02 | 0.02 |
| Others and unid. | 0.03 | 0.04 | 0.06 | 0.06 |
| Pisces | | | | |
| *Mallotus villosus* | + | 0.09 | 0.77 | 0.31 |
| *Boreogadus saida* | 0.01 | 0.03 | 0.01 | + |
| Gadidae | 0.01 | 0.09 | 0.03 | 0.01 |
| Others | 0.09 | 0.04 | 0.04 | 0.04 |
| Unidentified | 0.08 | 0.23 | 0.23 | 0.28 |
| Unidentified | 0.14 | 0.18 | 0.19 | 0.08 |
| Total | 0.93 | 1.18 | 1.76 | 1.13 |
| No. of stomachs | 862 | 1799 | 1012 | 2066 |
| Percent empty | 1.4 | 1.3 | 2.0 | 2.8 |

Table 4. Food of Atlantic cod (30-69 cm) on Hamilton Bank in autumn, 1977-82. Values are mean partial fullness indices.

| Trip number | 3[a] 1977 | 15 1978 | 27[b] 1979 | 44 1980 | 58 1981 | 71 1982 |
|---|---|---|---|---|---|---|
| Invertebrata (misc.) | 0.06 | 0.03 | 0.02 | 0.02 | 0.04 | 0.06 |
| Crustacea | | | | | | |
| Hyperiidae | 0.37 | 0.24 | 0.79 | 0.20 | 0.17 | 0.04 |
| Natantia | | | | | | |
| *Pandalus borealis* | 0.16 | 0.08 | 0.08 | 0.05 | 0.03 | 0.05 |
| Others and unid. | 0.12 | 0.15 | 0.06 | 0.07 | 0.09 | 0.09 |
| Reptantia | | | | | | |
| *Chionoecetes opilio* | + | | | 0.06 | 0.10 | 0.10 |
| Others and unid. | 0.02 | 0.03 | 0.01 | 0.03 | 0.04 | 0.01 |
| Others and unid. | 0.04 | 0.05 | 0.04 | 0.07 | 0.09 | 0.08 |
| Pisces | | | | | | |
| *Mallotus villosus* | 0.02 | | 0.02 | 0.24 | 2.06 | 0.62 |
| *Boreogadus saida* | 0.02 | 0.03 | 0.05 | 0.04 | 0.01 | 0.01 |
| Gadidae | 0.13 | 0.05 | 0.20 | 0.07 | 0.03 | + |
| *Reinhardtius hippoglossoides* | 0.68 | 0.03 | 0.06 | 0.01 | 0.01 | + |
| Others | 0.05 | 0.07 | 0.15 | 0.02 | 0.03 | 0.02 |
| Unidentified | 0.53 | 0.14 | 0.45 | 0.32 | 0.36 | 0.43 |
| Unidentified | 0.15 | 0.13 | 0.25 | 0.16 | 0.30 | 0.12 |
| Total | 2.31 | 1.03 | 2.17 | 1.35 | 3.34 | 1.63 |
| No. of stomachs | 91 | 175 | 92 | 302 | 293 | 697 |
| Percent empty | 1.1 | 0.6 | 2.2 | 2.3 | 1.0 | 0.3 |
| No. of sets | 10 | 17 | 11 | 29 | 41 | 72 |

[a] All sets were on the eastern or southeastern part of Hamilton Bank and about 40% of the stomachs came from a single set.

[b] No. sets were made in depths <200 m.

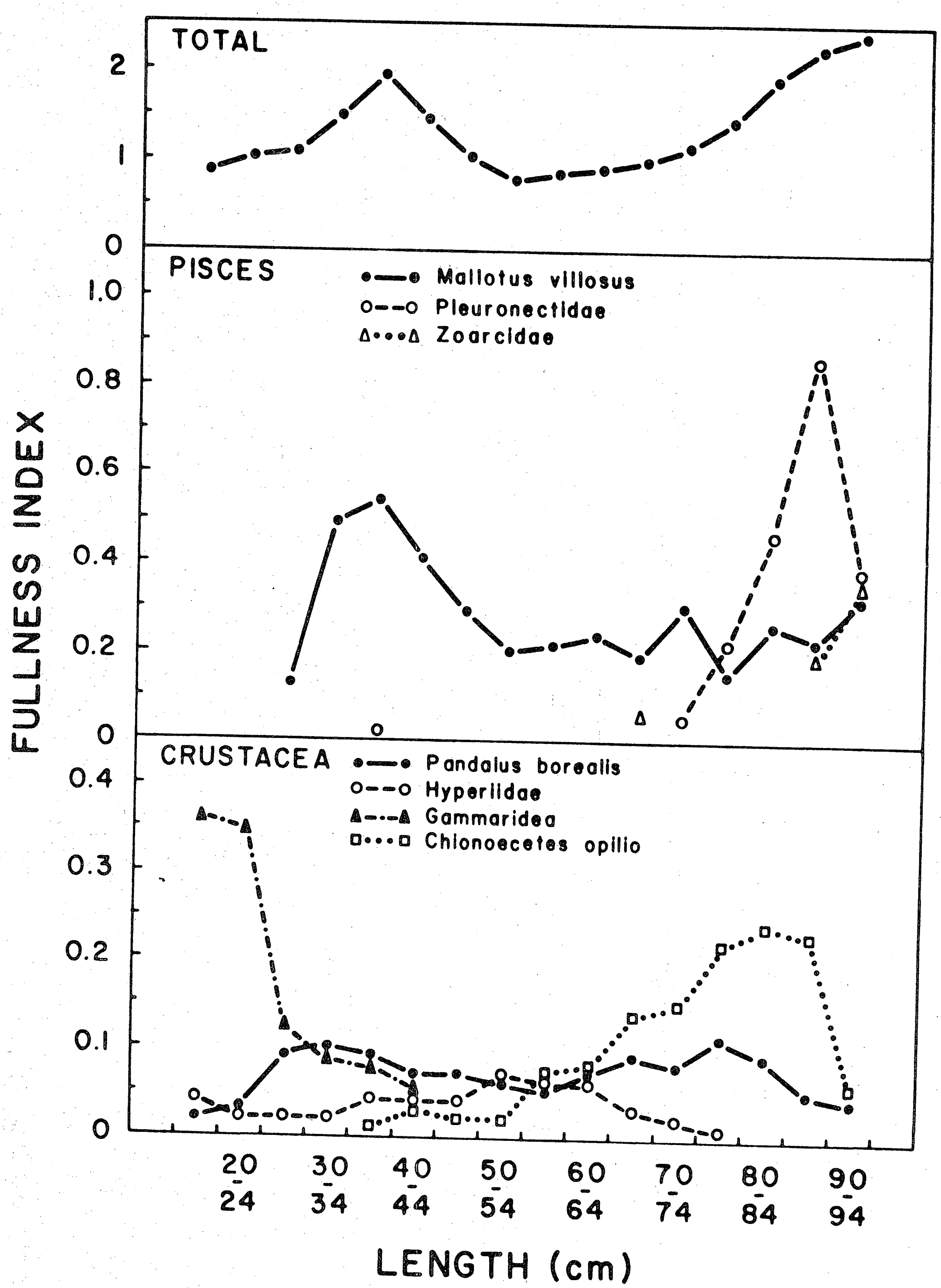


Fig. 1. Changes in total fullness index and partial fullness indices for major prey with increasing cod length in 1982.

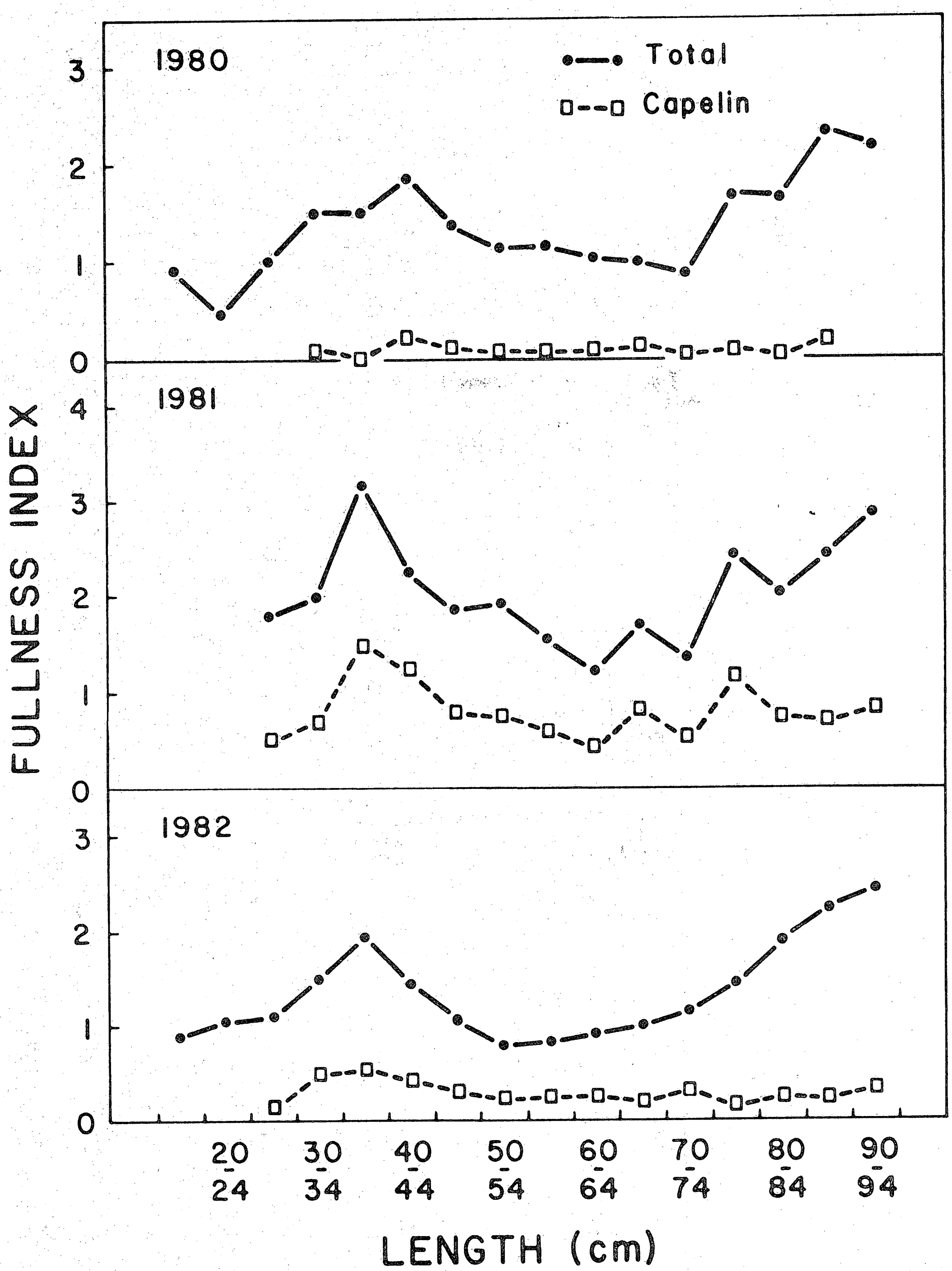


Fig. 2. Changes in total fullness index and partial fullness index for capelin with increasing cod length in 1980-82.

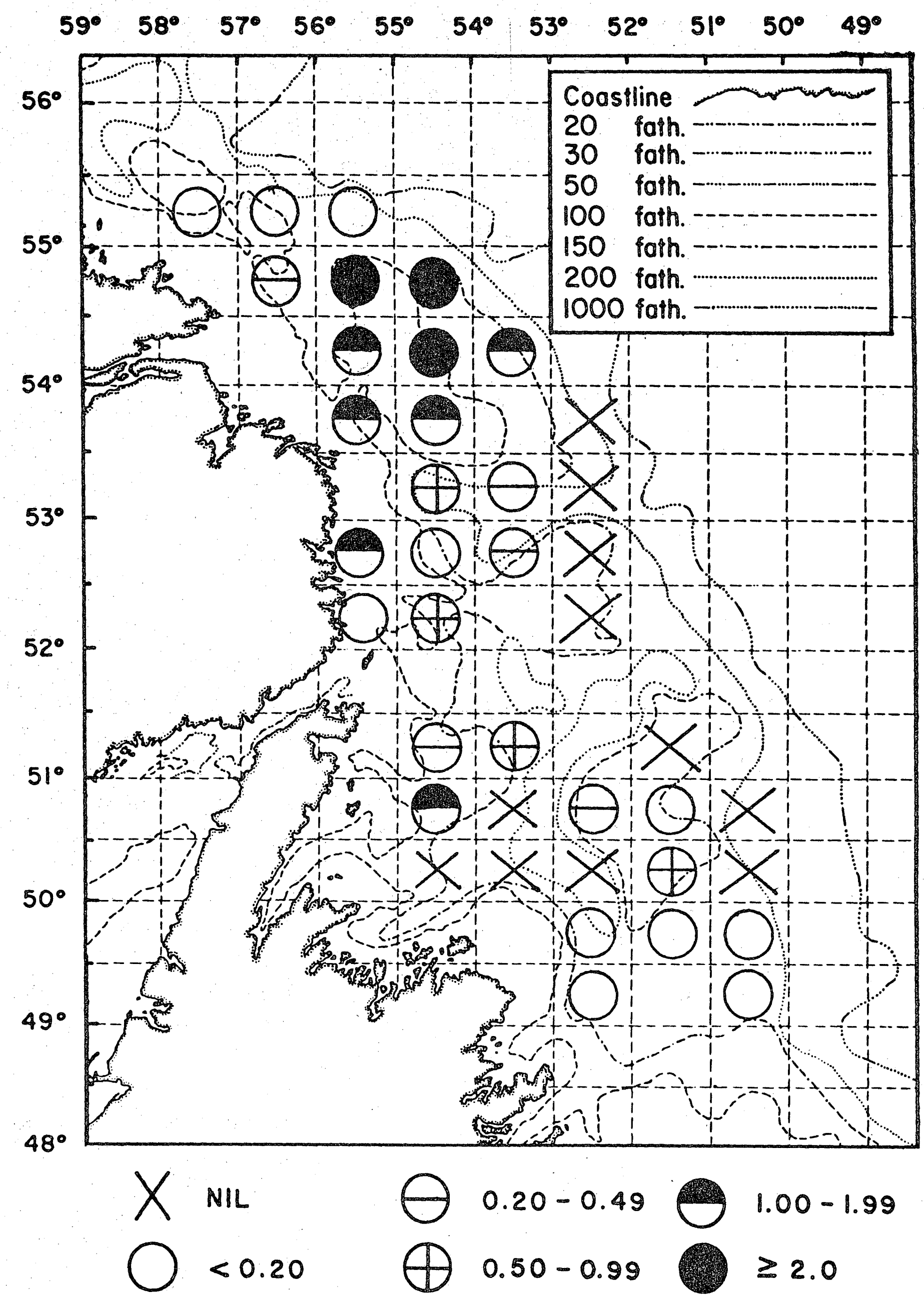


Fig. 3. Geographic variation in mean partial fullness index for capelin in 1981. All stomachs collected from cod (30-69 cm) caught in each 0.5° latitude x 1.0° longitude area were combined. Data from areas with fewer than 5 stomachs were not plotted. Many samples from between approximately 51°00'N and 52°30'N were lost.

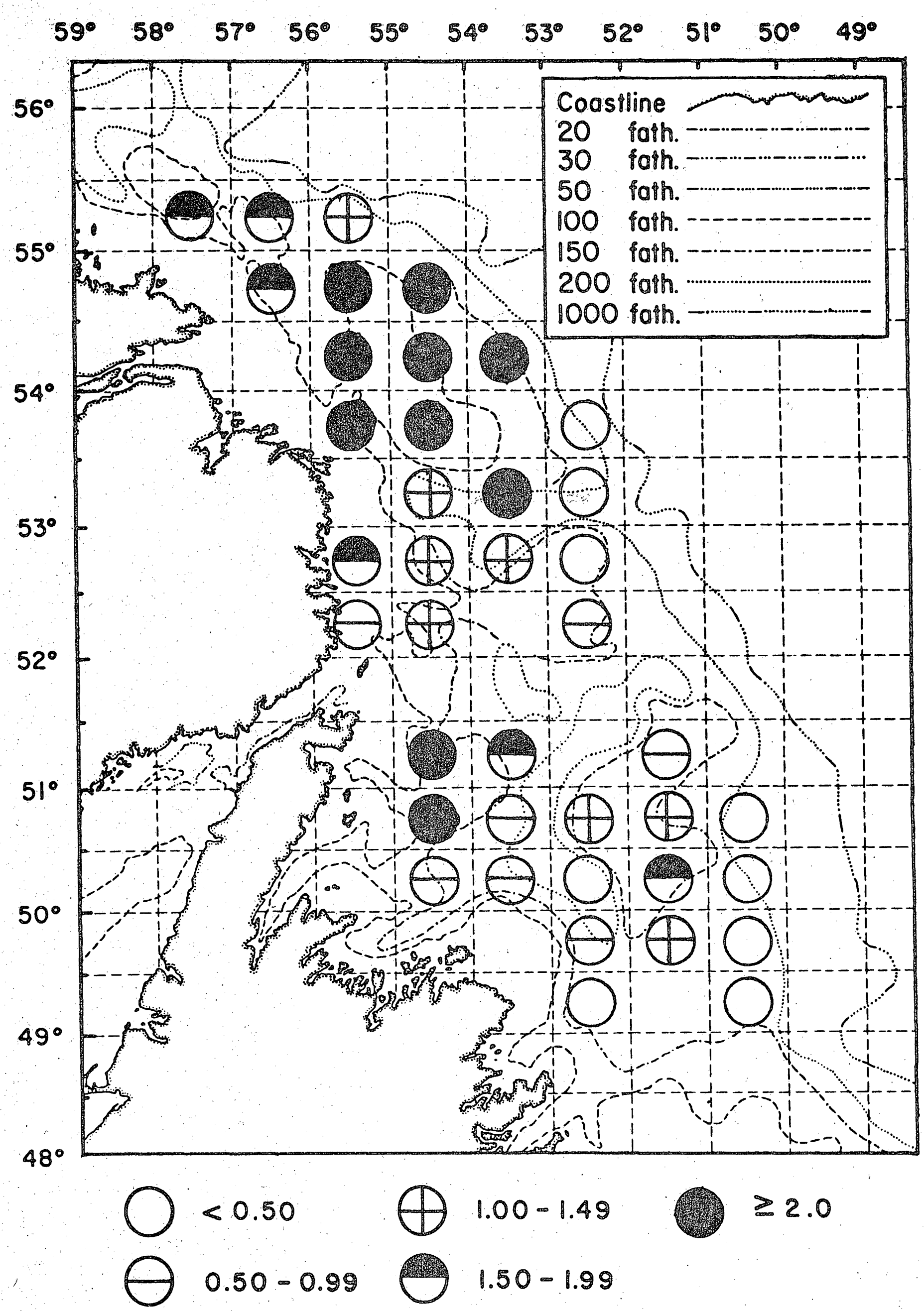


Fig. 4. Geographic variation in mean total fullness index in 1981. Some data set as displayed in Fig. 3.