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Northwest Atlantic Fisheries Organization

Serial No. N753

NAFO SCR Doc. 83/IX/87

FIFTH ANNUAL MEETING - SEPTEMBER 1983

Food of Atlantic Cod (*Gadus morhua*) on the Northern Grand Bank in Spring

by

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ABSTRACT

In May-June 1979 cod (Gadus morhua) on the northern Grand Bank (NAFO Div. 3L) were feeding on a wide variety of prey, but at least 66% of the diet by weight was accounted for by just five species: two planktivorous fish (sand lance, Ammodytes dubius, and capelin, Mallotus villosus), two crabs (Chionocoetes opilio and Hyas araneus) and the euphausiid Thysanoessa raschii. The importance of capelin (15% by weight) was low compared with the results of other studies off eastern Newfoundland and Labrador. Variability in stomach contents was attributable in part to differences in distribution of the various prey and to a gradual change in diet with increasing cod length. However, there was no strong preference for any of the major prey types. Catches of cod were highest in the south-central part of the Division, where stomach fullness was high, and in the north of the Division, where stomach fullness was very low. The northwestern edge of the Grand Bank plateau appears to be particularly favourable for cod feeding and may be an area of enhanced productivity.

INTRODUCTION

Predation by Atlantic cod, Gadus morhua L., on capelin, Mallotus villosus (Muller), is the trophic interaction of major concern at present to marine fisheries management in the areas of eastern Newfoundland and Labrador (NAFO Div. 2J+3K+3L). Capelin migrate to the shallow inshore waters to spawn in June and are preyed upon intensively by cod which arrive from the offshore banks at about the same time (Templeman, 1965; Lilly and Fleming, 1981). Cod which remain offshore also prey on capelin (Popova, 1962). Indeed, in offshore regions predation by cod on capelin continues at various times and locations throughout the year (Turuk, 1968, 1978; Stanek, 1973, MS 1975; Minet and Perodou, 1978; Lilly, 1982). This conspicuous interaction both inshore and offshore has led to the general hypothesis that cod are dependent on capelin.

An initial examination of the interaction between cod and capelin off northeastern Newfoundland failed to demonstrate any relationship between the growth of cod and the abundance of capelin (Akenhead, et al., 1982). Although it was clear that the lack of any demonstrable relationship might simply reflect inadequacy of the available data, it was also noted that cod feed on a wide variety of organisms and therefore may not be strongly linked to capelin. The strength of the interaction between cod and capelin can be determined only by experimentally manipulating abundances of the two species or, less satisfactorily, by monitoring the response of cod as capelin abundance fluctuates naturally over time. However, one may derive some insight into the strength of the interaction by determining the contribution of capelin to the diet of cod and by determining whether alternate prey are available and acceptable.

The purpose of this paper is to determine the food of cod on the northern Grand Bank in late spring when the cod-capelin association is thought to be particularly strong. The investigation focuses on the effects on cod diets of geographic variability and variability due to predator size. In addition, because the distribution of the various prey types on the northern Grand Bank is poorly known, the recovery of prey from cod stomachs might provide semi-quantitative information on the distribution of these prey taxa.

Study Area

NAFO Division 3L (Fig.1) covers the broad continental shelf off eastern and southeastern Newfoundland (46°- 49°15'N). This includes the northern part of the plateau of Grand Bank, with an extensive area less than 100 m in depth and high points of only 4 m depth on the Virgin Rocks. The plateau is separated from the Avalon Peninsula of Newfoundland by the Avalon Channel, which is part of a broad area between 100 and 200 m in depth extending to the east, west and particularly the northwest of the plateau. Depths greater than 200 m occur on the shelf to the north and on a gently sloping continental slope to the northeast and east.

The inshore part of the southward flowing Labrador Current, characterized by relatively cold, low salinity water, divides around the northern tip of Grand Bank, one branch passing through the Avalon Channel and the other along the eastern slope of the bank (Smith, et al., 1937). This results during late spring in cold (<0°C) water on the bottom at intermediate depths (about 100-150 m in 1979), with warmer bottom water in shallower and deeper regions (Fig. 1).

MATERIALS AND METHODS

SPECIMEN COLLECTION AND PREPARATION

Cod, capelin, and sand lance were captured during a stratified-random bottom-trawl survey of the northern Grand Bank (NAFO Div. 3L) in the period May 16-June 4, 1979, by the research side trawler A. T. Cameron equipped with a 41-5 Yankee otter trawl and the chartered research stern trawler Gadus Atlantica equipped with an Engel high-rise otter trawl. The codends were equipped with 29-mm mesh liners in both cases, and both ships trawled at 3.5 knots (108m/min) for 30 min at each fishing station. The two ships fished within about 1 km of each other during most of the survey, but each ship also made several sets unaccompanied by the other.

A stratified-random sample of five cod per 10 cm length-group was chosen for stomach content analysis from the catch of each set of the Gadus Atlantica. Most cod stomachs were excised at sea and preserved in 10% formalin, but some cod were frozen whole at sea and thawed in the laboratory before removal and preservation of their stomachs. 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 importance of the various prey types was assessed using three indices:

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

2) Percent weight (total weight of 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 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.

In calculating stomach fullness indices, length was used in preference to weight as a measure of predator size, because length is not influenced by changes in the weight of carcass, liver, gonads, and stomach contents. For examination of trends in stomach fullness with predator size, cod were combined into 10 cm length groups. Any group with fewer than 10 cod was excluded from the analysis.

From the basic set information, cod catches and catches of major fish prey were plotted on maps of the surveyed area. Partial fullness index values for some major prey groups were also plotted. General patterns of prey distribution and cod feeding were inferred from these figures.

DATA ANALYSES

The average amount of each prey type for all the cod in a set can be used to illustrate overall relationships, sometimes quite clearly. However, sets differed greatly in the numbers of stomachs collected and examined; a number of sets had few stomachs collected. Also the sizes of cod sampled differed substantially among sets. Therefore means of prey item amounts per set would necessarily reflect a heterogeneous class of things. Sampling variances about these means would be highly variable and often large; hence the means themselves would differ greatly in accuracy. Statistical analyses of such data would be of low power, and often inappropriate.

For our quantitative investigations, we used cluster analyses of the individual stomachs. The cluster analyses grouped individual stomachs by similarities in their PFI's for all the common food items. Common food items were those present in at least 2.5% of all stomachs examined. Empty stomachs, and stomachs containing only rare food items, were not used in the quantitative analyses. Where prey identification was done to different levels in different stomachs (due to degree of digestion of material), lower taxa were aggregated to genera or family level. The cluster analyses were used in conjunction with simulations of clusterings based on various neutral models. The neutral model simulations allowed us to determine expected values for various attributes of the clusters, under various specific hypotheses. For discussion of neutral models and ecological hypotheses, see Connor and Simberloff 1979, Pimm 1982.

For the clustering of the stomachs we used COMPCLUS, from the Cornell Ecology Package of quantitative ecological programmes (Gauch 1979). This fast clustering routine produces nonhierarchical clusters around randomly generated "seed" points. By changing the initial random number, different sets of random seeds, and hence potentially different clusterings, are produced. The iterative clusterings allow determination of robust associations within the data, and permit statistical analyses of the resultant clusters. Robust clusters are clusters that occur repeatedly across iterations, are defined by the same food items each time, and contain largely the same stomachs. The defining prey taxa for each cluster are determined in COMPCLUS by first ranking all prey taxa by their PFI values within each cluster. Those prey taxa required to account for 90% of the combined Fullness Index values for all the stomachs in a cluster are the defining or criterion prey for that cluster.

RESULTS

Distribution of cod, capelin and sand lance

Cod were taken in all but one of the successful sets (Fig. 2). Large catches (>150 kg) were common in deep water to the north, on the plateau to the south, and between these areas in the cold water of the northern Avalon Channel. Some large and moderate catches were also taken along the eastern slope of the Bank. Poorest catches tended to be in the east and southwest, particularly in the area where the cold core (<0°C) of the Labrador Current impinged on the bottom. Catch per-tow was not significantly correlated with either bottom temperature or depth ($P>0.05$). Capelin were taken in slightly more than half of the sets (Fig. 3). Largest catches were on the western part of the plateau and in the southern Avalon Channel. Capelin were also common in the north-central parts of the area. Capelin were not taken in sets on the eastern slope or along the northwestern Avalon Channel. Catches of sand lance were small. They were centered on the southeastern portion of the study area, but not on the slope itself (Fig. 4).

Prey Diversity: Qualitative

Cod preyed upon a wide variety of organisms (Appendix 1), but only a few species contibuted significantly to the total weight of stomach contents. Major prey were fish and crustaceans (Table 1). Two planktivorous fish, sand lance and capelin, comprised 43% of the diet by weight, and other fish plus unidentified fish comprised an additional 11%. The most important crustacea were crabs (Chionocoetes opilio, Hyas araneus), euphausiids (predominantly Thysanoessa raschii), shrimp (mainly Pandalus montagui), and gammarid and hyperiid amphipods.

For the stomachs examined, feeding was heaviest in the central and southern parts of the study area, and along the eastern slope of the bank (Fig. 5). The Total Fullness Index was usually low for cod taken in the northern part of the bank and along the Avalon Channel. Cod catch-per-tow was not correlated with total fullness index ($P > 0.05$), indicating that at the time of the survey the cod were not concentrated in areas where feeding was best. Considering the major prey taxa, capelin were found in the diets of cod in most sets from the eastern and central parts of the survey area (Fig. 6). Their contribution to the cod diet (reflected in the Partial Fullness Index) was highest in the central region, north of the Virgin Rocks. Capelin were not found in cod stomachs collected in the eastern part of the area, and in many sets taken in the northern edge of the bank. On the other hand, sand lance were a major contributor to the diet of cod in the eastern portion of the bank and along the southeastern slope (Fig. 7). They were present in stomachs of cod in many sets where sand lance themselves were not collected during the tow. Sand lance also made a substantial contribution to cod diets in the central portion of the bank, where feeding on capelin was also heavy. Of the various invertebrate taxa, crabs (both Chionocoetes opilio and Hyas spp.) and euphausiids were of special interest. Feeding on those taxa was widespread, with the PFI of crabs high in western and central sets, and moderate in most sets from the Avalon Channel (Fig. 8). The distribution of cod feeding on euphausiids showed a similar distribution, with largest PFI values near the northwestern edge of the plateau of Grand Bank (Fig. 9).

It is apparent from Fig. 6-9 that cod were feeding on several different prey taxa, and not exclusively on capelin, or even capelin and sand lance. Those figures do not give a complete picture of the diversity of cod diets, as there are several other taxa which also constitute a substantial part of the food of cod, in at least some of the sets. The listing of the foods of cod in Table I shows some of the prey diversity, but the listed categories are coarse for most invertebrates. Twenty-nine taxa of prey met our criterion of common food item (present in at least 2.5% of all stomachs examined), and many of those taxa were families or orders, rather than species (Appendix). Furthermore, Fig. 6-9 show some evidence of spatial separation of feeding, for example feeding on sand lance along the slope and feeding on crabs in sets from the northwestern edge of the bank. However, especially in the central and southern parts of the study area, where cod catches were largest, heavy feeding was observed on several different prey taxa. Clearly, more quantitative analyses are necessary to resolve patterns and preferences in cod feeding.

Prey Diversity: Quantitative

The clustering runs reinforce the impression of extensive heterogeneity in the diets of cod. Over 10% of all the stomachs were clustered with no more than 2 other similar stomachs. Nonetheless, large clusters did occur, and these clusters were robust across clustering iterations.

How orderly is the pattern of cod diets in these cluster analyses? Fig. 10 shows the expected frequency of clusters of various sizes under 2 extreme hypotheses. If the 1771 stomachs had been divided into 402 clusters on purely random grounds (reflecting unselective feeding on randomly occurring prey of variable abundance) most of the clusters would have contained between 2 and 8 stomachs, with clusters containing more than 32 stomachs being exceedingly rare. On the other hand, if the sizes of the 402 clusters reflected the proportional occurrence of the various food items in all the stomachs (reflecting highly selective feeding on at least all the common food items), large clusters would have been common. The mean across the 20 clustering iterations of 189 unique stomachs per clustering run is much larger than expected under either extreme hypothesis, whereas the frequency of large clusters is intermediate between the extremes. We conclude that there is evidence of significant preferential feeding on some prey or groups of prey (more large clusters than expected from a random partition), but most individual cod have heterogeneous diets (many of the stomachs contain diets that are either unique or occur in small clusters, and fewer large clusters exist than the occurrence of common food items allow.)

The conclusion that individual cod often have diverse diets is emphasised because the criteria for clustering of many of the large clusters reflects the presence of several prey types, rather than a single kind of prey. Over half of all the large (more than 16 stomachs) clusters use the presence of between 3 and 5 types of prey as defining criteria (Fig. 11). Nonetheless, clusters defined by a single prey type in the stomachs are common, with usually 8 different single criterion clusters occurring in each iteration. These reflect 8 different types of prey on which numbers of cod were feeding exclusively when captured. We can infer that diets of cod are more ordered than chance associations of prey, because groups of randomly chosen stomachs contain significantly more types of prey than do our actual clusters (Fig. 12). Nonetheless, both the commonness of clusters defined by the presence of several prey types and the variety of types of single prey clusters indicate that cod consume a highly heterogeneous diet.

The 8 unique food item clusters contain a diverse array of defining prey types, including both major prey fish (capelin and sand lance) and several types of invertebrates, including queen crab, gammarids, hyperiids, euphausiids, polychaetes and Pandalus shrimp. In the clusters defined by the presence of more than one type of prey, combinations of these same prey types predominate consistently. There were on average 26.15 large clusters with a total of 75.4 diagnostic prey per iteration. 85% of these diagnostic prey designations were occurrences of the same 8 prey types which occurred as single diagnostic prey types in the single prey type clusters. Hyas crabs were rarely the only food found in cod stomachs, and hence did not designate a large single-prey type cluster. However, adding Hyas to the 8 other common criterion prey types account for about 90% of all diagnostic prey types of large clusters. The occurrence of other uncommon prey types in the large clusters does not differ from the occurrence of uncommon food items in equivalently sized groups of randomly selected stomachs (Table 2).

We conclude that there are clearly major prey taxa identifiable for these cod. However, there are 8 or 9 such groups, rather than just a few, and these major prey types are fed on in a variety of combinations, as well as in some cases exclusively. There are two initial variables that might help clarify the patterns of diversity and variation in cod diets within these data. Cod show size selective feeding, and may show geographic variation in feeding. The geographic variation could reflect variation in availability of preferred and alternate prey, geographic variation in the size of cod (and hence be a secondary reflection of size selective feeding) or actual geographic variation in feeding preferences. Without data on prey availability we can attempt only preliminary investigations of these patterns of variation in diet, but some noteworthy patterns are found.

Size Selectivity: Qualitative

The intensity of predation on major prey categories, as determined from mean partial fullness indices, varied with the length of the cod (Fig. 13). Euphausiids were preyed upon most intensively by small cod; sand lance and capelin by medium-sized cod (40-69 cm); crabs by large cod (60-79 cm); and flatfish by the largest cod ($\geq$80 cm). However, each major prey category was preyed upon by the complete size range of cod, and there were no abrupt changes in diet with increasing cod length. Total fullness index was highest in medium-sized cod (40-69 cm).

Size Selectivity: Quantitative

The size selectivity of cod feeding can also be investigated with the clustering runs. Knowing the overall proportion of cod of each size (10 cm groupings), we can assess whether the proportion of cod whose stomachs occur in clusters of interest are a representative sample of the entire population collected. A priori, we predict that large cod are predominately piscivorous, whereas small cod feed more heavily on invertebrate prey.

For clusters defined by feeding at least partially on capelin, there are marginally significant differences between observed and expected numbers of cod of each size class ($0.05<P<0.06$). For cod feeding at least partially on sand lance, the same marginally significant difference is present($0.01<P<0.05$). In both cases, the differences are attributable to a paucity of very small cod, but not to a noticable surplus of large ones (Fig. 14). On the other hand, clusters based on presence of queen crabs (alone or in combination with other prey) are a highly nonrandom sample from the overall length distribution ($P<0.001$). Large cod occur in these clusters much more frequently than expected.

Cod feeding exclusively on invertebrates other than crabs tend to be small cod significantly more often than expected by chance ($P<0.001$), although large cod were found feeding exclusively on these invertebrates. Euphausiids are of particular interest, and for clusters defined by their presence (alone or in combination with other prey), the length distribution of cod is a representative sample of the overall length distribution of sampled cod ($P>0.50$).

The relatively small sizes of individual clusters required that several clusters be combined for the Chi-square analyses. Hence, specific relationships of size to foraging preferences could have been obscured in the mixed diet clusters. We used simulations to produce expected numbers of cod of each length class in each of the single prey type clusters. We randomly partitioned the original data into groups with memberships equal to the numbers of cod stomachs in the actual clusters. Over 500 such random partitions we were able to specify the probability of observing any specific number of cod of any length group in clusters of specific sizes. Thereby, we were ably to determine if size specific preferences for particular prey types were present in the single prey type clusters.

For both cod feeding exclusively on capelin and cod feeding exclusively on sand lance, larger fish occur significantly more frequently than expected (Table 3). For the cod from the various "pure" invertebrate clusters, small cod occur significantly more frequently than expected in the gammarid and polychaete clusters, and marginally more frequently than expected in the hyperiid cluster. Large cod are not significantly infrequent in any of the clusters. Hence, although there is clear evidence of some degree of size dependent feeding in cod, the pattern is not rigid. Small cod eat fish frequently, especially in combination with invertebrate prey, whereas large cod also feed extensively, and sometimes exclusively, on invertebrates.

Regional Variation: Quantitative

The clusters determined by the analyses of the stomach contents data can be associated directly with the specific defining prey types, as described above. Geographic patterns in cod predation then can be investigated by determining which sets contained cod assigned to clusters defined by the presence of prey taxa of interest. Hence, geographic relationships which, in an overall investigation may be obscured because of diverse sizes of cod in a single set or because the track of a set might have covered more than one feeding concentration of cod, can be investigated with greater specificity using the cluster results.

Capelin feeders are concentrated on the western and central portions of the survey area. More specifically, cod feeding solely on capelin are found primarily in the northwestern portion of the area, with other cases scattered south and west along the 100 m contour. Cod feeding on capelin in the southern and central parts of the region generally are feeding on a mixed diet of capelin and various invertebrates, or also on both capelin and sand lance. (Fig. 15).

Cod feeding on sand lance tend to occur east of those feeding on capelin. Cod feeding exclusively on sand lance are generally in the southeastern portion of the study area. Cod consuming a mixed diet of sand lance and invertebrates are distributed across a wider area, and are intermixed with cod feeding exclusively on capelin (Fig. 16).

Cod feeding exclusively on queen crab are common in the northwestern edge of the bank. They also occur along the southern edge of the study area, where they occur along with cod consuming a mixed diet of crab, sand lance, and various other invertebrates (Fig. 17). Cod feeding exclusively on smaller invertebrates are widespread across the region. Those feeding exclusively on gammarids are common along the northern portion of the Bank; euphausiid feeders are common along the coast of the Avalon Peninsula and the nose of the bank; hyperiid feeders are most common along the outer slope of the bank (Fig. 18).

The distributions of clusters by set also can be used to provide more detailed insights into selection among different potential prey. The probability of individual sets containing cod classified into different clusters (that is, sets with cod feeding on different foods) can be calculated directly as the product of the independent probabilities of sets being present in each of the clusters being considered. Observed joint occurrences can then be compared to expected numbers, and interactions among possible diets can be assessed directly. For these calculations, we included all sets providing at least 5 stomachs used in the cluster analyses.

Fewer sets contain cod feeding on both capelin and sand lance than is expected by chance, regardless of whether one considers cod feeding exclusively on capelin, exclusively on sand lance, or mixed diets of either type of prey (Table 4). However, the differences between observed and expected values are small, and not statisticaly significant (P=0.073). There are also usually few joint occurrences of cod feeding exclusively on sand lance and other cod feeding exclusively on any of the invertebrates. Although the differences are again small, the preponderence of deviations in the same direction from expected values (consistently too few occurrences) is significant with a binomial test (P=0.038). On the other hand, there are slightly, but significantly more joint occurrences of exclusive capelin feeders and cod feeding on the various pure invertebrate diets, than expected by chance.

It seems that whereas cod feeding on sand lance do so preferrentially to feeding on invertebrates, cod feeding on capelin commonly occur with other cod feeding exclusively on invertebrates. Some information on relative availability of the major fish and invertebrate prey is required before a more complete interpretation of these findings is possible.

However, it is clear that cod show no strong preference for any of the prey types examined. Individual fish commonly consumed mixed diets, and fish in close proximity to each other often consumed quite different prey. The distributions of the various prey are clearly not uniform across the study area, but the dissimilar distributions of prey did not lead to extreme partitioning of diets among cod from different areas. Rather cod with differing diets occurred together as often, or nearly as often, as expected by chance.

DISCUSSION

Cod on the northern Grand Bank fed on a wide variety of organisms, but five species (sand lance, capelin, queen crab, a toad crab (Hyas araneus), and a euphausiid (Thysanoessa raschii)) comprised at least 66% of the stomach contents by weight and 68% of the total fullness index. The tendency of cod to feed on many taxa but concentrate on relatively few crustaceans and fish, particularly in the colder regions of its distribution, is well documented (see, for example, the review by Klemetsen (1982)).

Capelin were important to cod only in the central and southwestern regions of Div. 3L. They represented only 15% of the total cod diet by weight, compared with approximately 30% estimated in previous studies (Campbell and Winters, 1973; Minet and Perodou, 1978). The value of 15% is probably a low estimate for the annual contribution of capelin to the diet of the 2J+3KL cod stock. The present study was restricted to Div. 3L, the southeast of which is a major centre of sand lance abundance (Winters, 1983). These schooling planktivorous fish are about the same size as capelin, and are fed upon intensively by cod of the same size range as feed on capelin (Lilly and Fleming, 1981; this study). North of the Grand Banks sand lance are very minor prey whereas capelin are reported to be the major prey (Popova, 1962; Turuk, 1968; Minet and Perodou, 1978). Hence, for the 2J+3KL cod stock as a whole, sand lance would be less important and capelin more important than reported here for Div. 3L alone.

A second factor which might affect the relative importance of capelin is the timing of the survey. By late May early June many maturing capelin will have left the northern Grand Bank in their migration to spawning grounds on the southern Grand Bank (Kovalyov and Kudrin, 1973), while others might have moved closer to the coast in preparation for shore spawning in late June-July (B. Nakashima, pers. comm.). Cod feed intensively and almost exclusively on capelin in inshore waters in June-July (Templeman, 1965; Lilly and Fleming, 1981), and also in deep (>200 m) water north of Grand Bank in winter (Lilly and Fleming, 1981). A more accurate estimate of the contribution of capelin to the diet of cod requires seasonal information on cod distribution and feeding.

A third factor which might affect the importance of capelin is capelin abundance. Capelin stocks were depressed in 1979 following a series of weak year-classes (Bakanev, MS 1981; Carscadden et al., MS 1981). Perhaps more capelin are consumed when they are more abundant. We need to know the functional relationship between feeding rate and prey availability, and whether cod aggregate in areas of capelin abundance and actively pursue capelin schools.

The other major prey of cod in Div. 3L are crustaceans. Crabs appear to be more important than in most other areas, although they are locally important prey of cod in parts of the southern Gulf of St. Lawrence (Walwood and Elner, MS 1982). The importance of crabs may be overestimated, for their chitinous exoskeletons might retard digestion and evacuation from cod stomachs compared with unarmoured endo-skeletal animals such as fish.

Euphausiids were preyed upon most intensively near the northwestern edge of the plateau of Grand Bank. Intensive feeding by even large cod on such small prey indicates that the euphausiids must be very abundant and accessible, possible forming swarms undertaking diel vertical migrations which bring them close to the bottom.

Cod on the northwestern edge of the Grand Bank plateau feed well at several levels in both the grazing and detrital food chains. Euphausiids, planktivorous fish and crabs are all abundant. Further study is required to determine if this is an area of enhanced productivity, and whether a high proportion of the production reaches the benthos.

Gradual changes in prey taxa with increasing cod length were noted in this and many previous studies (eg. Powles, 1958; Rae, 1967; Daan, 1973; Minet and Perodou, 1978; Lilly and Fleming, 1981). These changes clearly reflect preference for large prey (Daan, 1973), and are a consequence of energetic advantages associated with the selection of large prey (Kerr, 1971; Wankowski and Thorpe, 1979) and a morphological limitation on maximum prey size (Wankowski, 1979). However, prey size is not the only factor influencing prey selection, for even euphausiids were moderately important for large cod. Several thousand euphausiids were occasionally found in stomachs of cod >80 cm in length. It is highly likely that abundance or availability of prey is important in prey selection (Allan, 1981), but this cannot be examined at present because independent quantitative information on prey abundance and availability at the time of sampling are lacking. One of the biggest challenges in studying feeding behaviour of cod on the Grand Banks is assessing the abundance and horizontal and vertical distribution of the prey.

When benthic and pelagic prey can be simultaneously examined at a single site, it will be possible to examine more thoroughly variation in individual feeding behaviour. Cod caught in a single tow often differ considerably in their prey composition. Much of this variation may be related to spatial variability over the distance traversed by the trawl (about 3 km). Nevertheless, there may be specialization on specific prey types or specific regions of the habitat, as described for trout (Bryan and Larkin, 1972) and bluegill (Werner, et al., 1981). Pearcy et al. (1979) deduced from stomach contents and collections of prey in midwater and bottom trawls that cod in Balsfjord, Norway, exhibited two different feeding behaviours: pelagic feeding and benthic feeding.

Analytically, stomach contents data have been problematic. The use of fullness indices seems to overcome one major problem; providing a measure of the diet components which is not dominated by either extremely numerous small prey or a few very large ones. The use of cluster analysis avoids many potential analysis problems posed by the unequal abundances of different prey types, and the non-normal distributions of prey types which are common. A single cluster analysis alone cannot provide statistical answers to many ecological questions. Used iteratively, however, and used in conjunction with neutral model alternative clusterings, statistically valid inferences can be drawn directly. These inferences are legitimate, regardless of the distribution of prey indices among stomachs and sets, and the sparseness of prey type by stomach matrices.

The analytic methods used in this study led to a number of statistically supported and specific conclusions about cod feeding. Cod feed on a variety of prey, and individual cod often have quite varied diets. There is some size selectivity in cod feeding, and also some geographic variation, but neither relationship is strong. Within a single set, different cod may be feeding on quite different prey. Each of these generalizations might have been possible without using the quantitative methods presented here. However, the use of these methods provides the additional empirical support desired in scientific studies, without requiring that unwarranted assumptions about distributions and central tendencies of the data be made. Further study with these and other data will be necessary to determine whether the quantitative methods can provide truly novel insights into feeding and predator prey-relationships.

ACKNOWLEDGEMENTS

We wish to thank C. Bauld for examining cod stomachs, C. Mullins for examining stomachs and drafting the figures, and R. Foster for assistance with computer programming.

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Table 1. The food of cod on the Northern Grand Bank, May - June, 1979.

	Percent[a] Frequency	Percent by weight	Mean PFI
Mollusca		1.4	0.03
Misc. Invertebrates and Unidentified		2.4	0.07
Crustacea			
Amphipoda		3.0	0.11
Euphausiacea		9.1	0.27
Natantia		2.4	0.08
Reptantia		27.0	0.52
Other and Unidentified		0.3	0.01
Pisces			
Mallotus villosus	19.1	15.0	0.43
Ammodytes dubius	19.8	28.0	0.74
Miscellaneous		9.1	0.11
Unidentified		2.3	0.06
TOTAL		100.0	2.43
No. of Stomachs: 1898			
Percent empty: 2.4			

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

Table 2. For random samples of size N from the total of 1771 stomachs (all stomachs containing at least 1 food item that appeared in at least 2.5% of all stomachs), the number of times out of 20 random partitions that specific types of prey were criterion food items. Also the number of other prey types that were criterion food items occasionally in these random partitions.

Prey Type	# of occurences out of 20 iterations for clusters of size: N = 70	45	20
Ammodytes (Sand lance)	20	20	20
Mallotus (capelin)	20	20	18
Euphausiids	20	20	17
Chionocoetes sp.	19	20	14
Hyas sp.	20	20	14
Gammarids	15	12	9
Pandalus sp.	12	9	3
Hyperiids	10	8	9
Number of other types of prey occurring in:			
1 iteration out of 20	6	7	9
2 iterations out of 20	1	2	1
3 iterations out of 20	2	4	0
4+ iterations out of 20	0	1*	0

*Ascidacea was a criterion food type in 7 of the iterations.

Table 3. To test size selectivity of cod diets reflected in specific clusters, the 1771 stomachs were partitioned into groups matching exactly in numbers the clusters present in a representative COMPCLUS run. The table presents the observed (OBS) number of cod of each 10 cm length category that were present in each cluster, and the cumulative proportion (C.P.) of the 500 iterative random partitions with the observed number or fewer members of each length category. Length classes abundant in the observed cluster will have high C.P.'s, whereas, length classes rare in the observed clusters will have low C.P.'s.

Criterion	Length Class (cm)					
Prey (N)	20-39	40-49	50-59	60-69	70-79	80+
Gammarids (78)						
Obs	16	20	18	15	8	1
C.P.	.988*	.396	.186	.602	.842	.072
Ammodytes (50)						
Obs	3	5	20	10	5	7
C.P.	.224	.006*	.944	.602	.708	.998*
Chionocoetes (42)						
Obs	1	0	1	19	15	6
C.P.	.004*	.000*	.000*	1.00*	1.00*	1.00*
Mallotus (40)						
Obs	3	11	9	6	4	7
C.P.	.408	.890	.158	.210	.660	.994*
Hyperiids (38)						
Obs	6	14	8	9	1	0
C.P.	.894	.996*	.332	.556	.078	.056
Euphausiids (27)						
Obs	5	5	9	5	3	0
C.P.	.940	.428	.854	.510	.564	.090
Polychaetes (20)						
Obs	4	8	4	1	2	1
C.P.	.958*	.992*	.396	.066	.732	.608
Ammodytes + Mallotus + Euphausiids + Gammarids (44)						
Obs	1	15	14	8	3	3
C.P.	.040*	.980*	.604	.452	.408	.730

. . . Cont'd.

Table 3. (Cont'd.)

Criterion Prey (N)	Length Class (cm) 20-39	40-49	50-59	60-69	70-79	80+
Mallotus + Euphausiids + Hyperiids + Pandalus (39)						
Obs	4	16	8	9	1	1
C.P.	.600	.998*	.192	.576	.078	.220
Ammodytes + Hyperiids + Isopoda (29)						
Obs	3	5	17	3	1	0
C.P.	.564	.333	1.00*	.078	.120	.114
Chionocoetes + Euphausiids + Gammarids (27)						
Obs	0	1	13	5	4	4
C.P.	.044*	.014*	.998*	.494	.776	.946
Hyas + Polychaetes (16)						
Obs	0	2	1	10	3	4
C.P.	.080	.118	.010*	1.00*	.894	.984*

*Cumulative proportions less than 0.05 and greater than 0.95 are marked to illustrate particularly unlikely numbers of cod at length in the clusters.

Table 4. The number of sets containing at least 1 cod whose stomach was classified into specific clusters of interest. Also, the expected joint occurrences in the same sets of stomachs from different clusters, under the hypothesis the distributions of stomachs by set was independent of cluster membership.

Type of Cluster (defining food)	Number of sets
Total with more than 3 stomachs used	120
Pure sand lance	28
Pure capelin	26
Pure queen crab	23
Pure gammarids	34
Pure hyperiid	15
Pure euphausiids	17
Pure polychaetes	15
Sand lance (pure or mixed diet)	60
Capelin (pure or mixed diet)	50
Queen crab (pure or mixed diet)	32
Any pure invertebrate group	64
Any pure or mixed invertebrate group, but no fish	82

Joint occurrences on the same set

Diet	Obs	Expected
Pure capelin with pure sand lance	4	6.07
Pure capelin with any sand lance	10	13.00
Any capelin with pure sand lance	9	11.67
Any capelin with any sand lance	27	25.00

Various Invertebrate diets	Pure capelin		Pure sand lance	
	Obs.	Exp.	Obs.	Exp.
Pure Gammarids	9	5.67	4	7.93
Pure Hyperiids	2	2.50	3	3.50
Pure Euphausiids	5	2.83	4	3.97
Pure Polychaetes	4	2.50	0	3.50
Gammariids + Polychaetes + Hyperiids + Isopoda	7	3.83	2	5.37
Gammarids + Polychaetes + Euphausiids	6	2.33	5	4.67
Gammarids + Euphausiids + _Pandalus_	3	2.67	0	3.73
Gammarids + Euphausiids	4	2.83	3	3.97

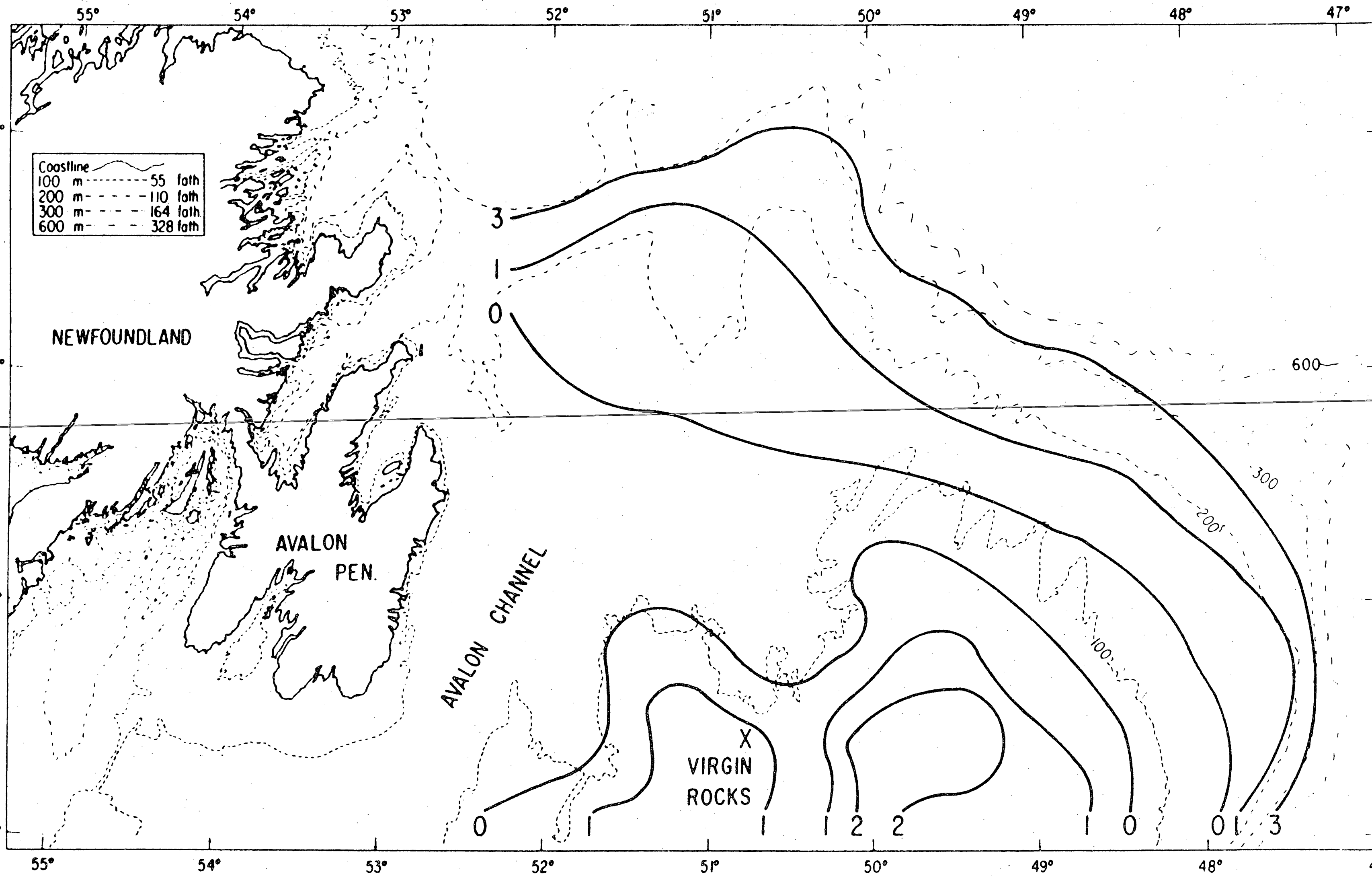

Fig. 1. NAFO Div. 3L, showing place names mentioned in the text and the approximate positions of bottom isotherms in May-June 1979.

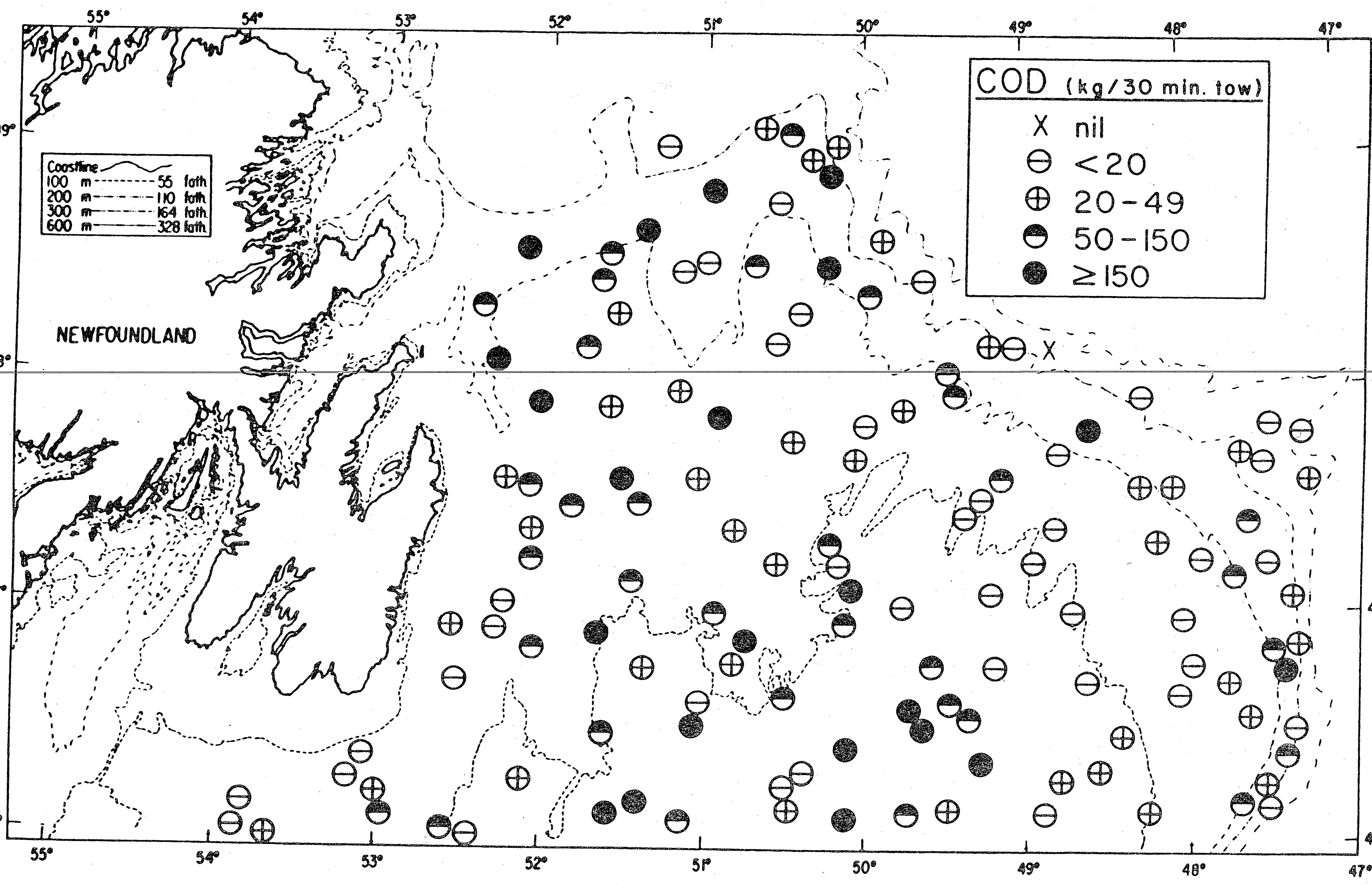

Fig. 2. Cod catches in NAFO Div. 3L during Gadus Atlantica trip 21, May-June 1979.

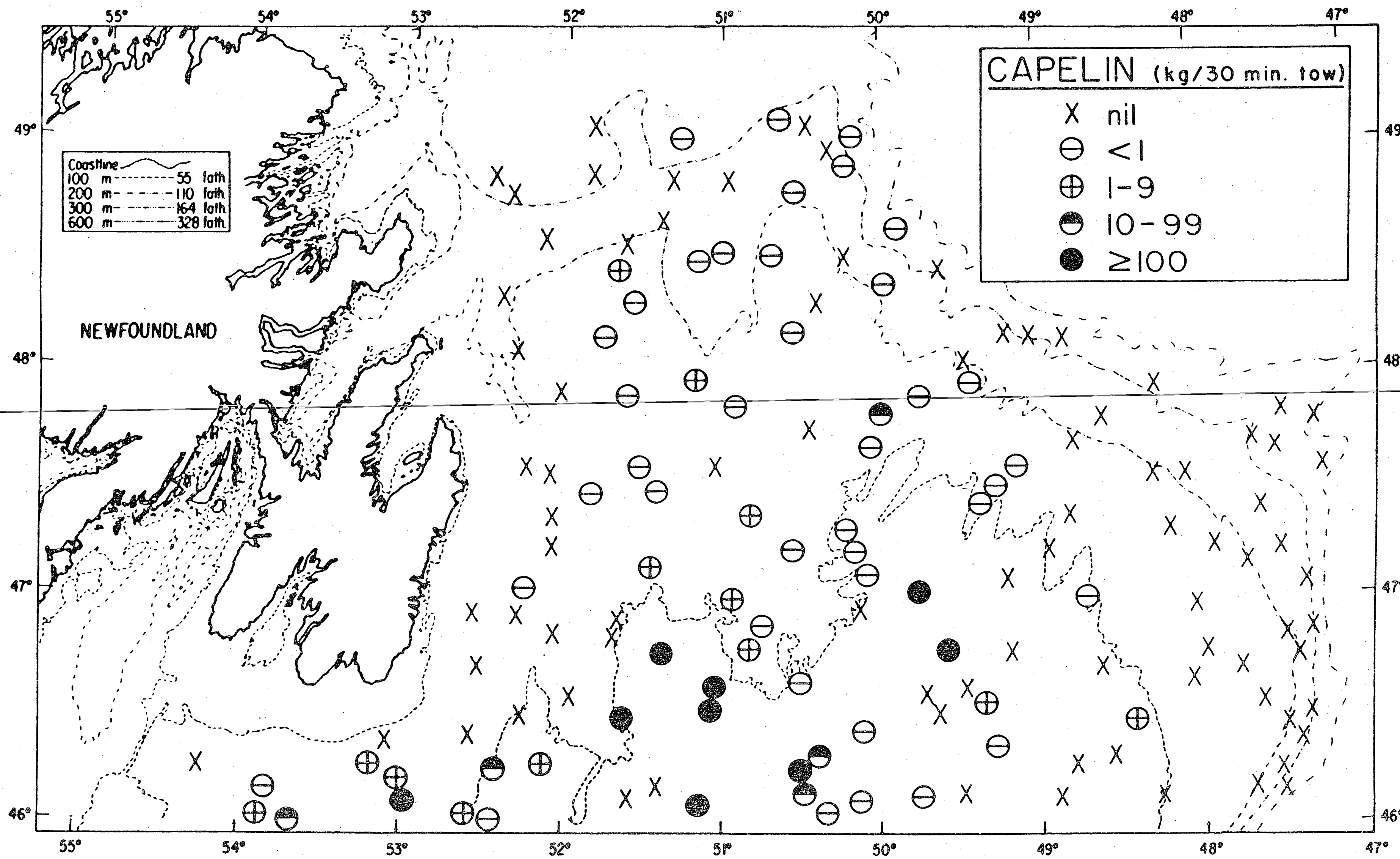

Fig. 3. Capelin catches in NAFO Div. 3L, May–June 1979. The larger of catches by the <u>Gadus Atlantica</u> and the <u>A. T. Cameron</u> is shown for each position.

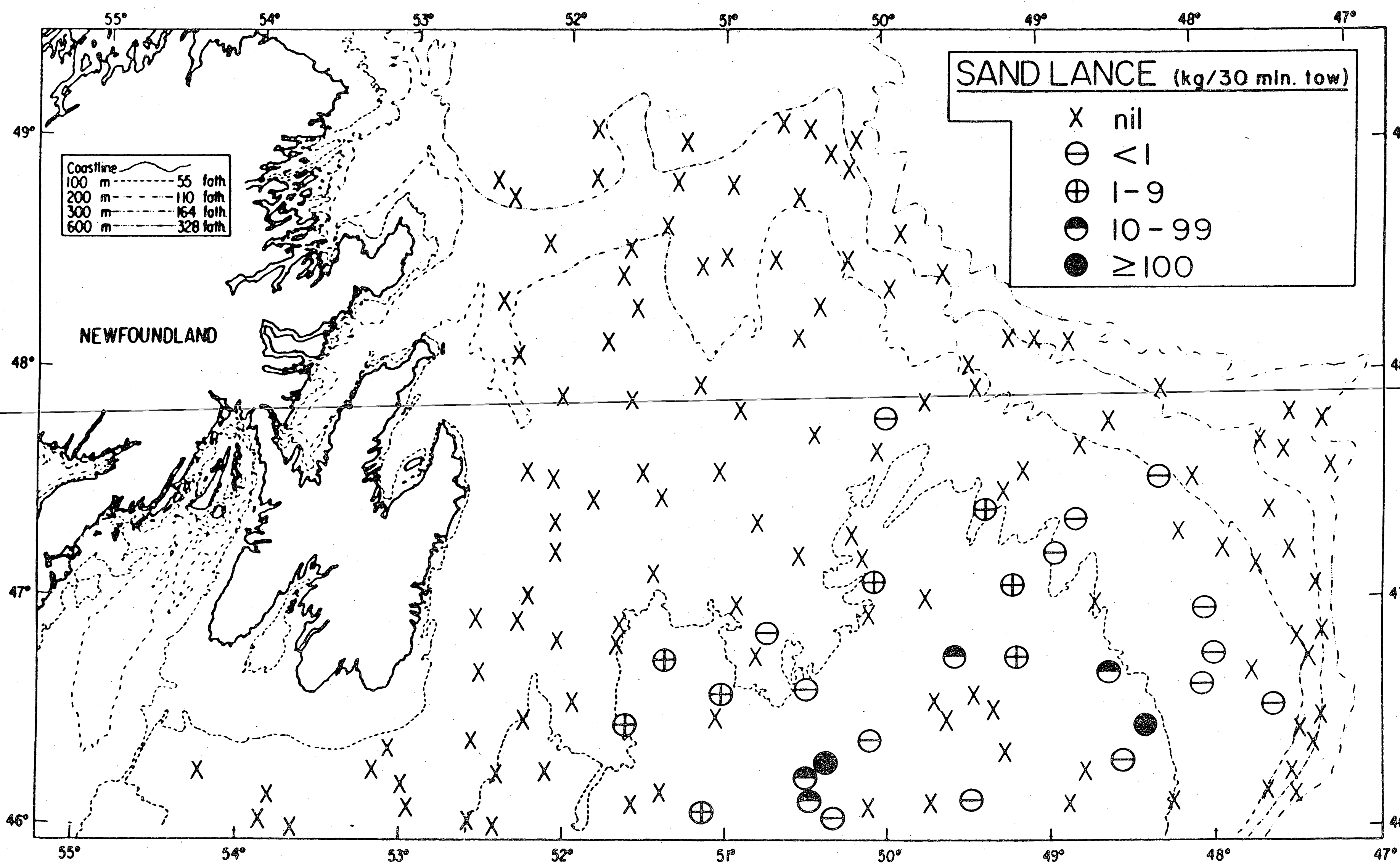

Fig. 4. Sand lance catches in NAFO Div. 3L, May-June 1979. The larger of catches by the _Gadus Atlantica_ and the _A. T. Cameron_ is shown for each position.

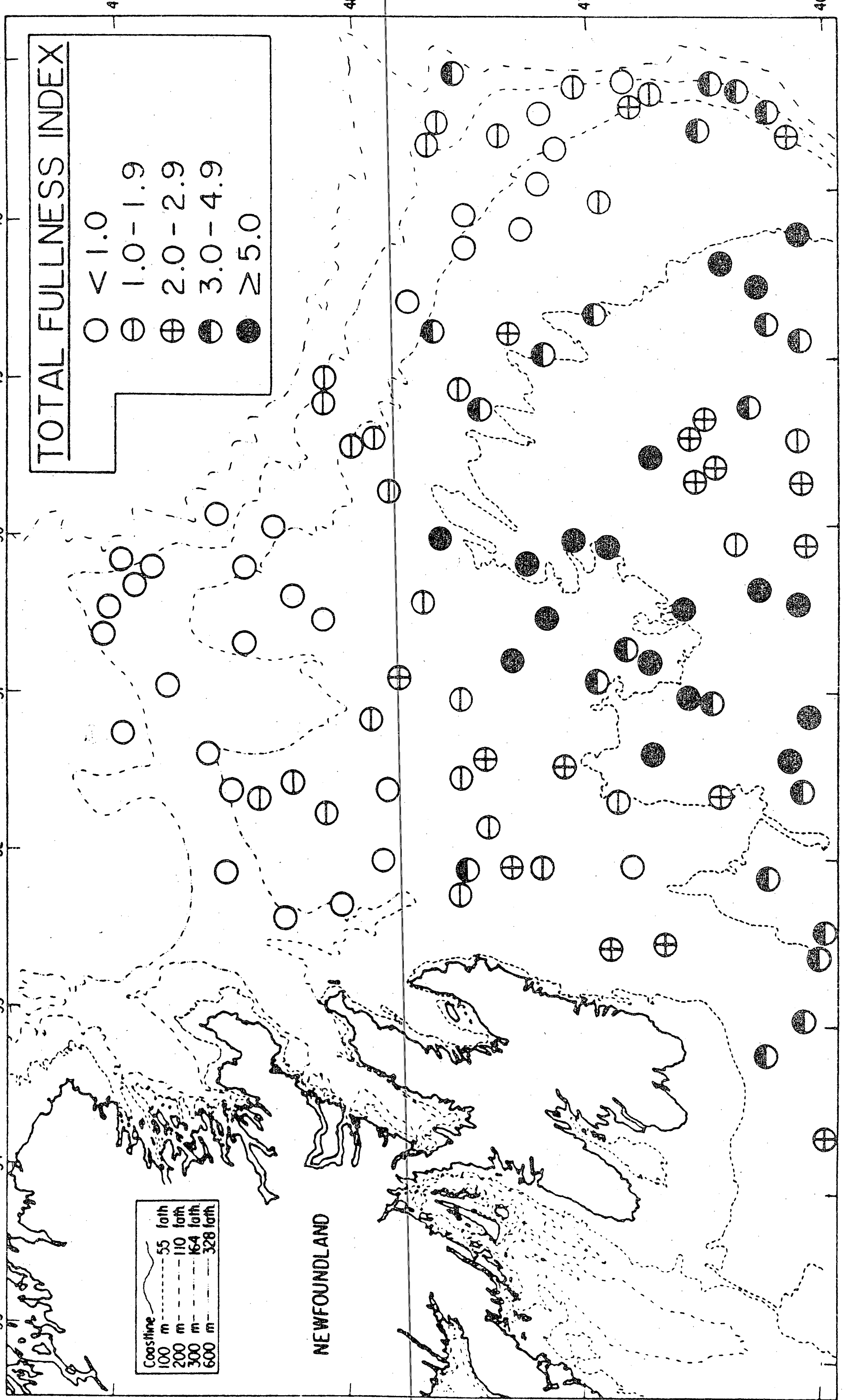

Fig. 5. Total fullness index of cod by set.

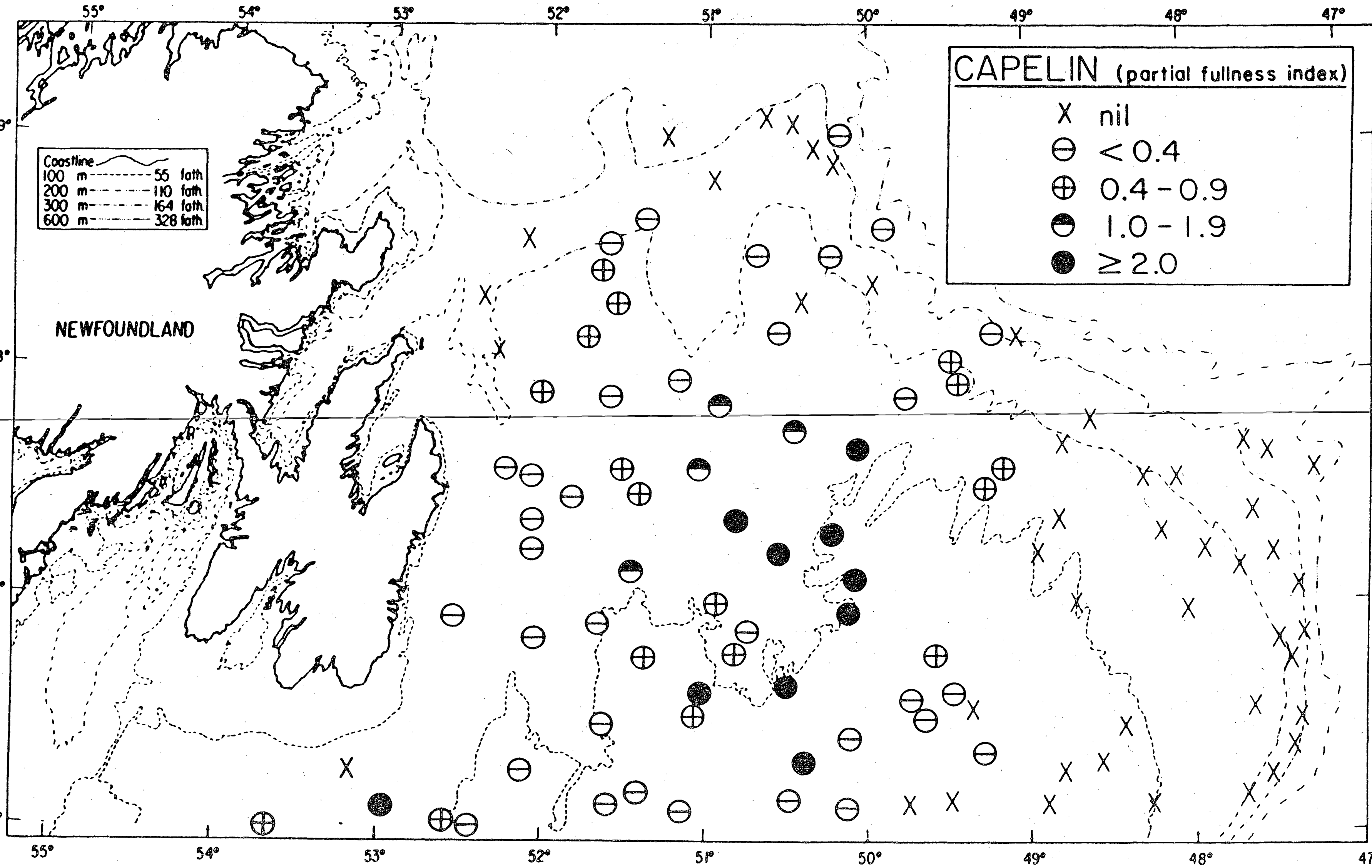

Fig. 6. Partial fullness index of capelin by set.

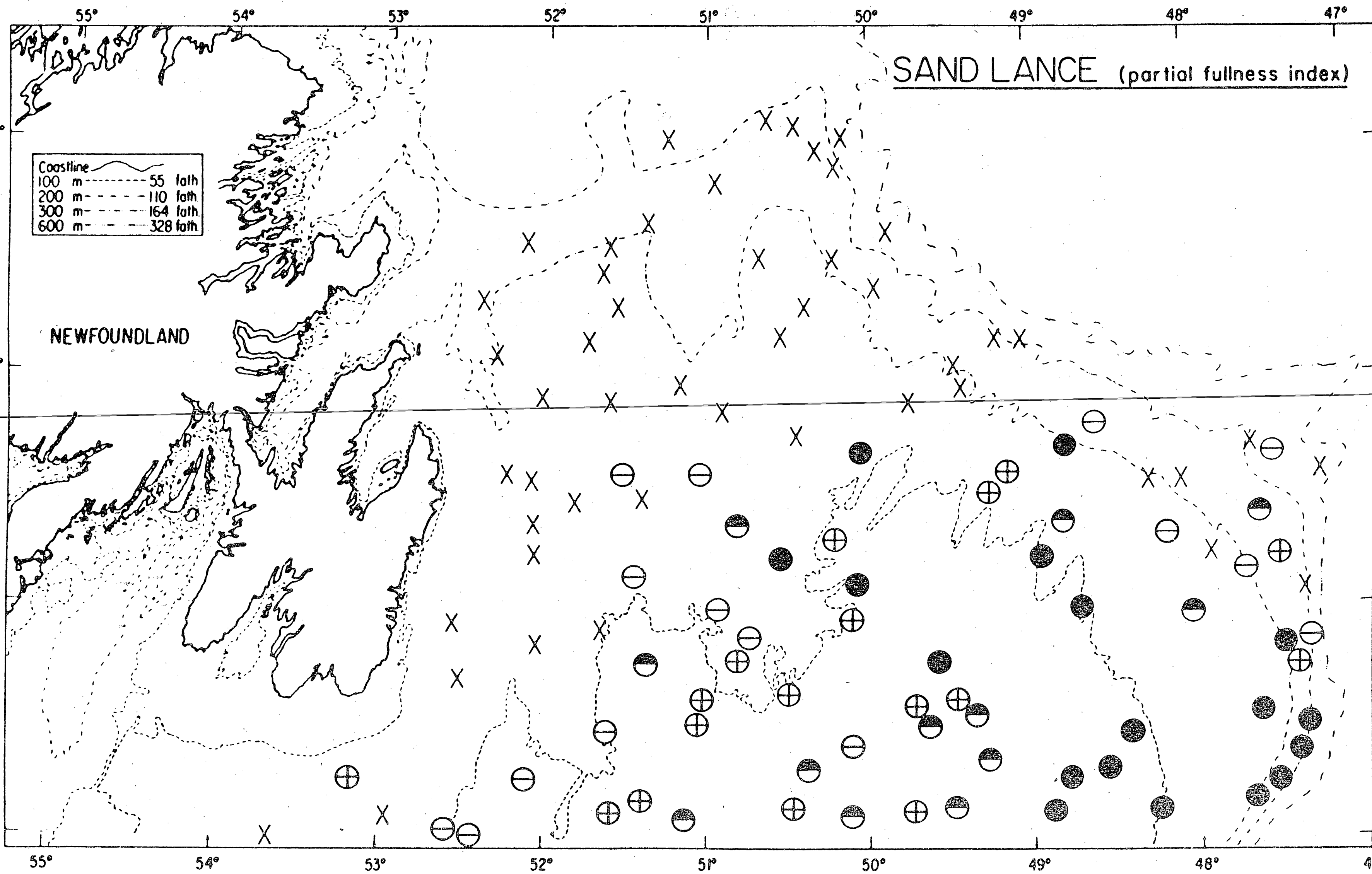

Fig. 7. Partial fullness index of sand lance by set. Symbols as in Fig. 6.

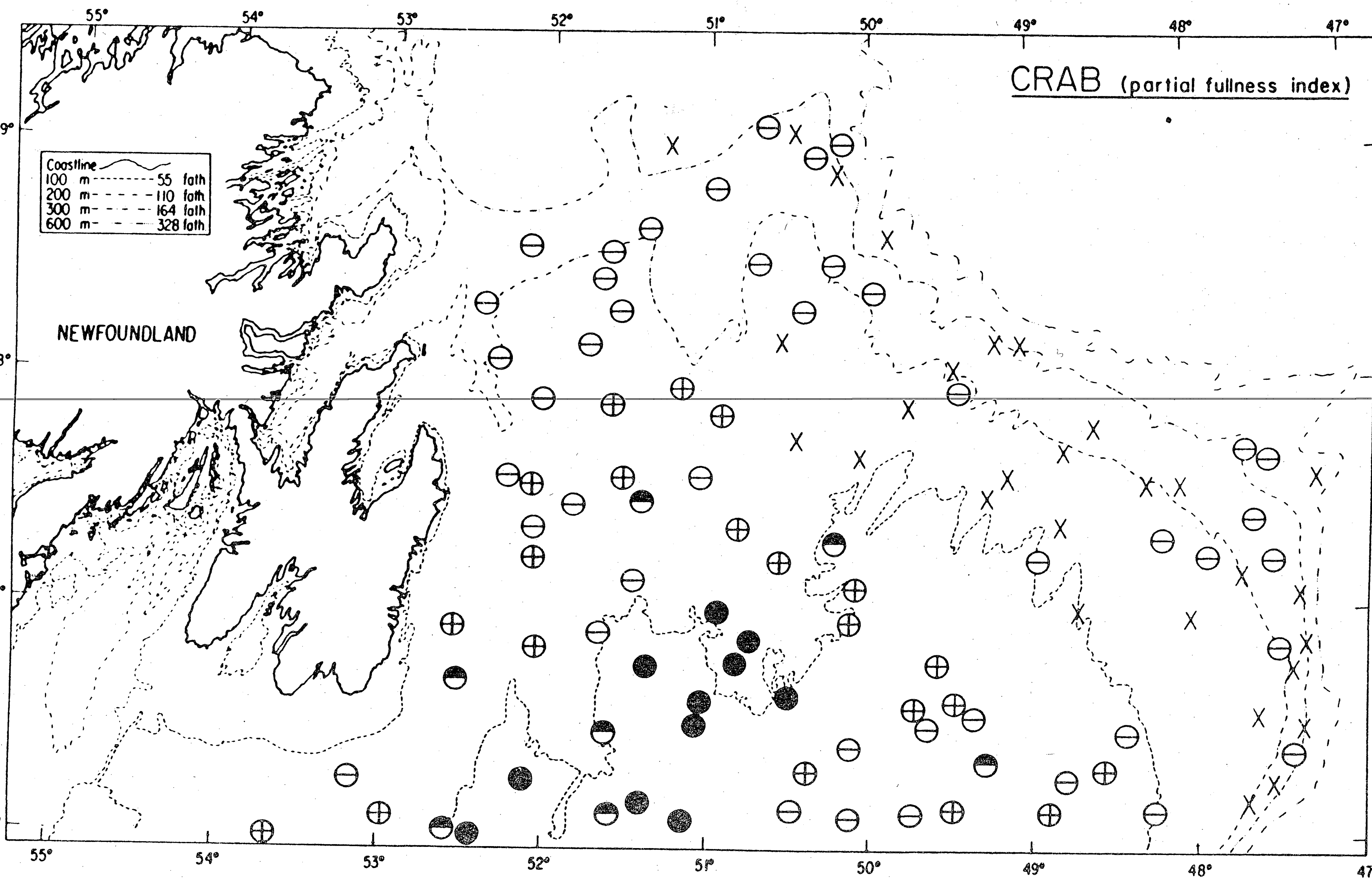

Fig. 8. Partial fullness index of crabs by set. Symbols as in Fig. 6.

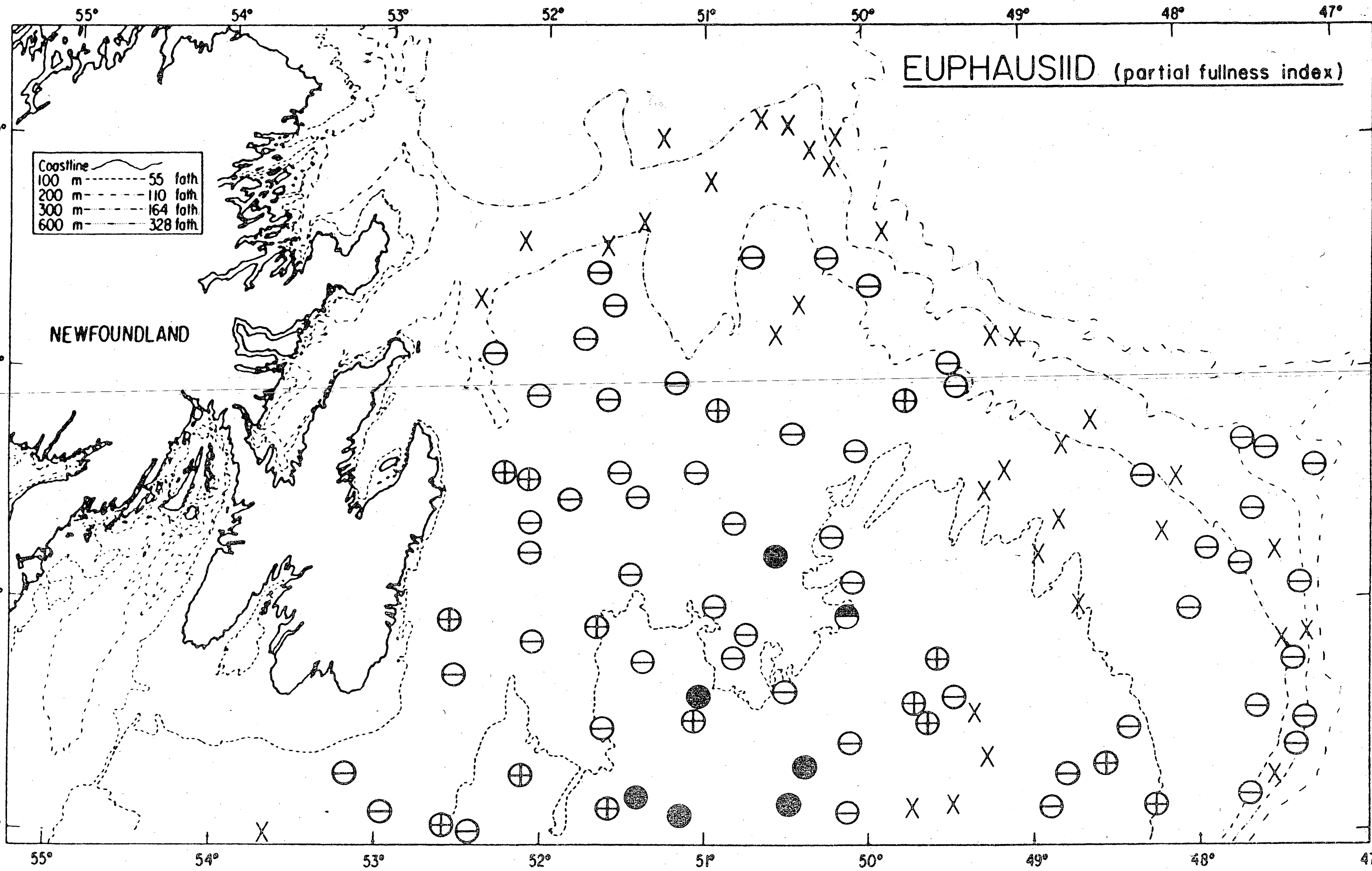

Fig. 9. Partial fullness index of euphausiids by set. Symbols as in Fig. 6.

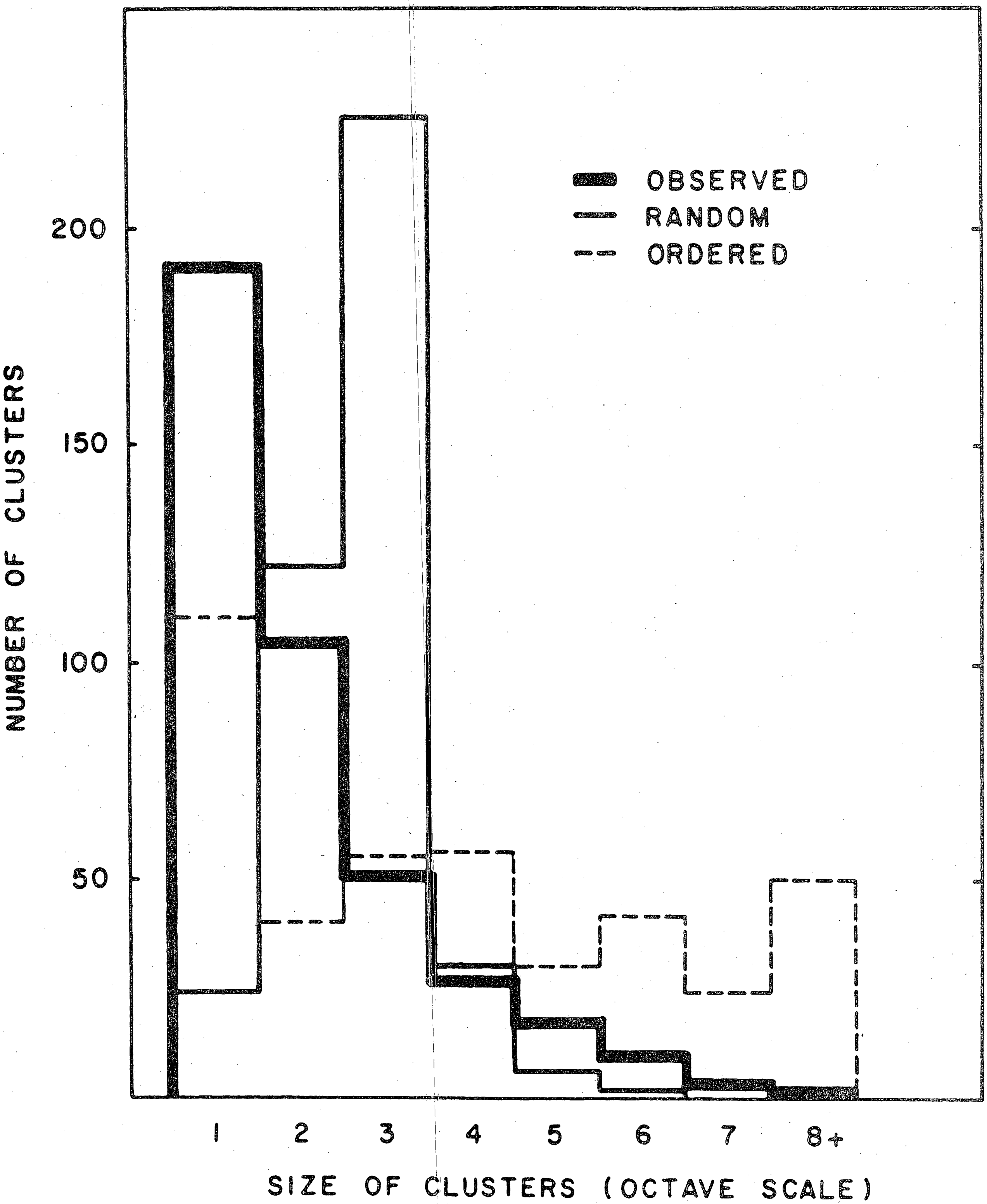

Fig. 10. Observed number of clusters of various sizes (wide line), from repeated COMPCLUS runs on the 1771 cod stomachs containing at least 1 common food item. Values are mean (across 20 clusterings) for number of clusters of each octaval size, where "octaves" are, 1 stomach, 2-3 stomachs, 4-8, 9-16, 16-32, 33-64, etc. (see Pielou 1979 for discussion of octave classes in species-abundance studies). Also plotted are expected number of clusters of each size group under a completely random hypothesis (narrow line), and a completely selective hypothesis (dashed line).

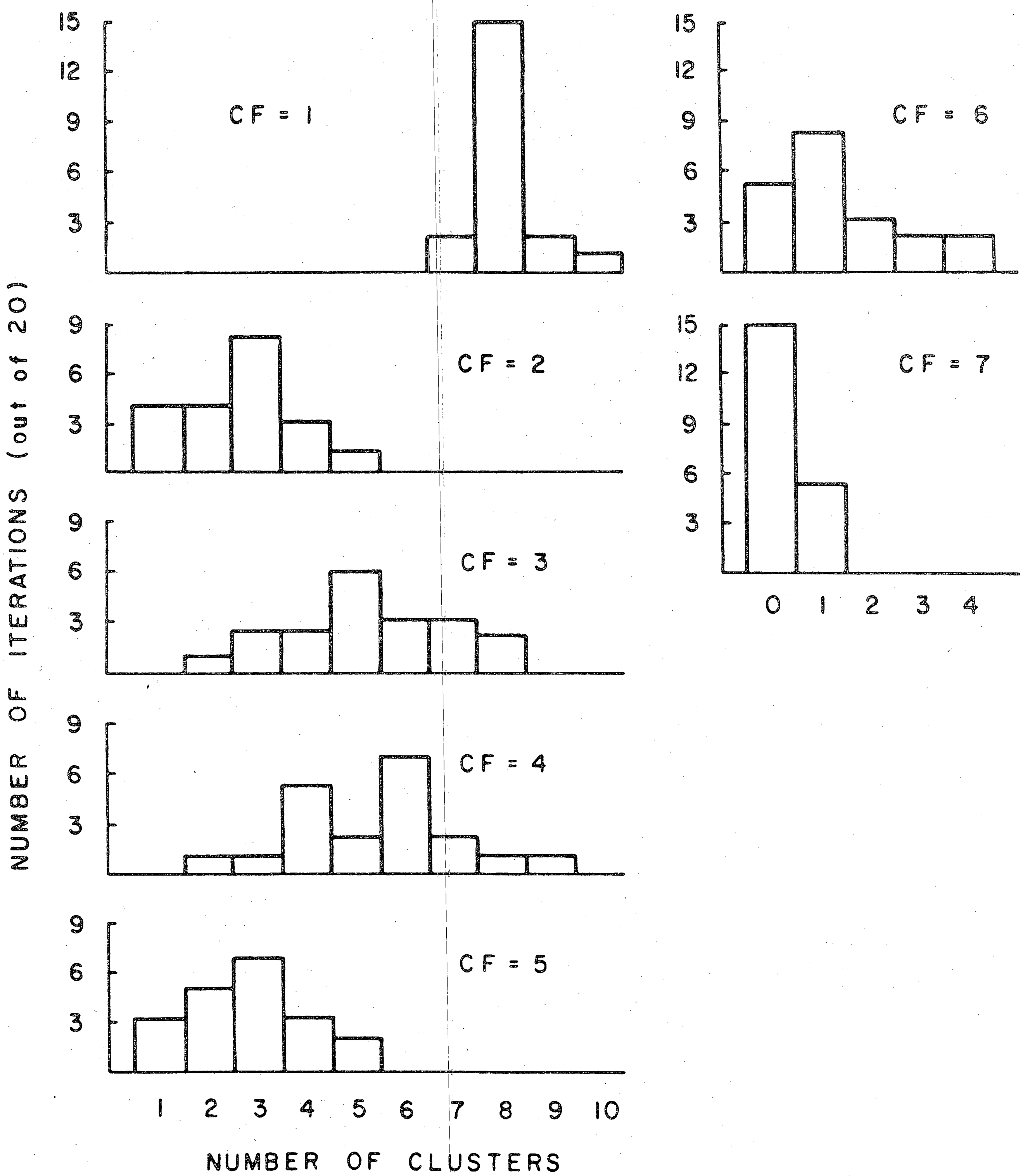

Fig. 11. For the 20 repeated clusterings of the cod stomachs by food contents, the number of times that clusters with various numbers of criterion foods (C.F.) occurred. For example, the first graph, for C.F. = 1 (one criterion food) shows that 15 of the 20 runs had 8 clusters with a single defining food, 2 runs had 7, 2 runs had 9 such clusters, and one run had 10 clusters defined by a single food.

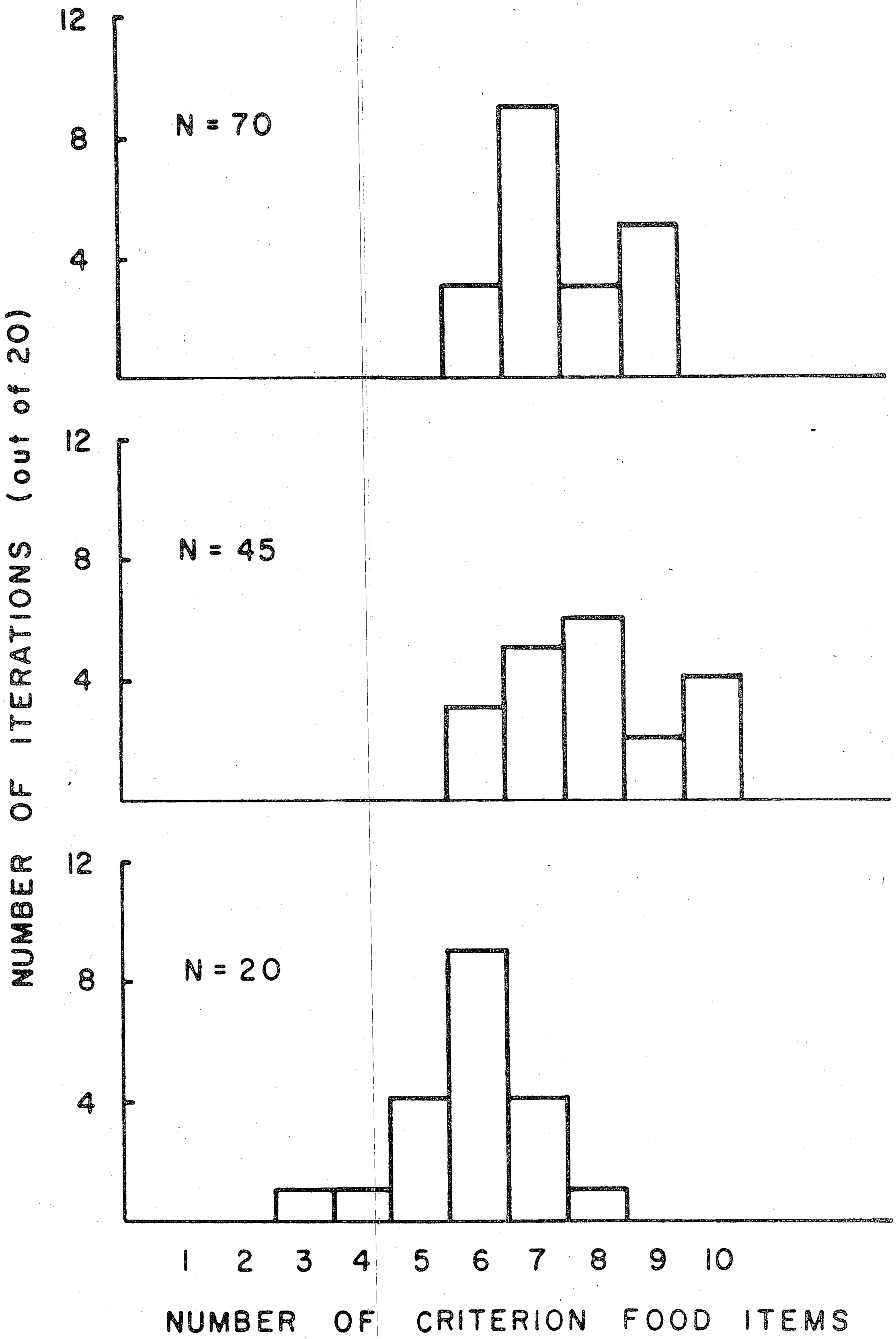

Fig. 12. For 20 random samplings for the cod stomach data, the number of times that samples of sizes N had various numbers of criterion prey types. For example, in 20 samples of 70 stomachs, 6 prey taxa were required to account for 90% of the summed PFI in 3 samples, 7 prey items were required to meet the criterion in 9 samples, 8 prey taxa were required in 3 samples, and 9 prey taxa were required to meet the criterion in 5 samples.

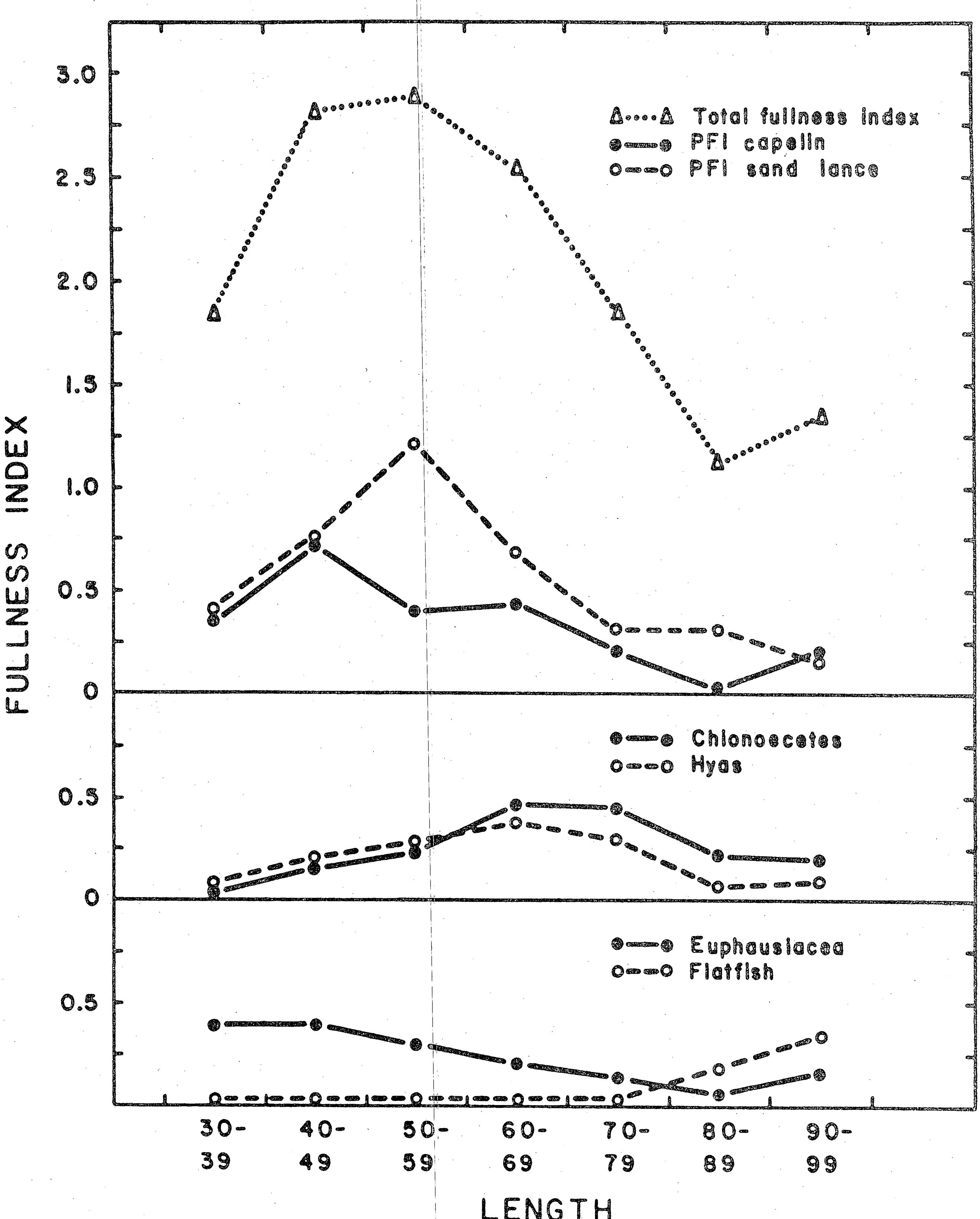

Fig. 13. Changes in total fullness index and partial fullness indices for major prey with increasing cod length.

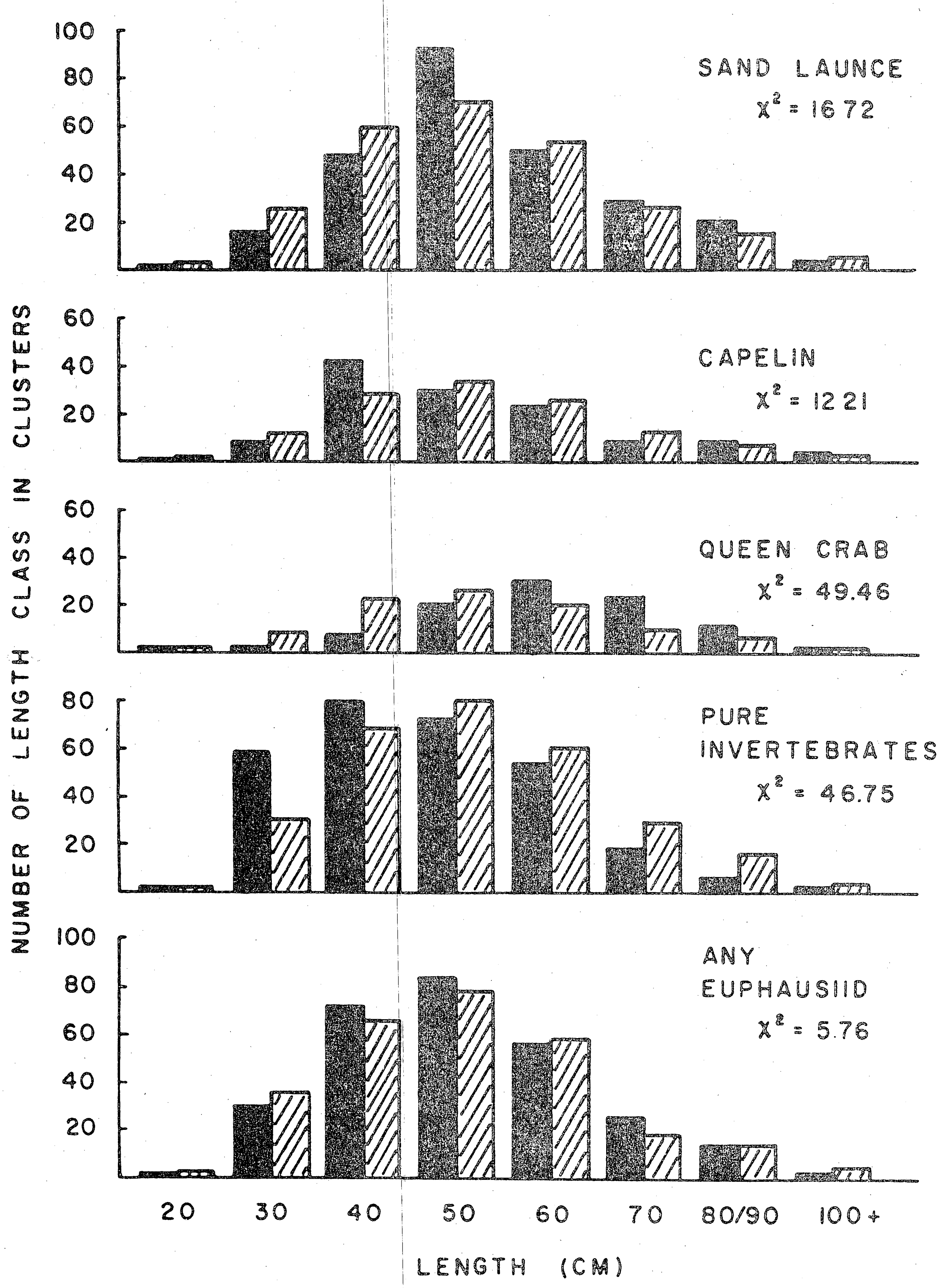

Fig. 14. From the actual distribution of lengths of cod in the total sample, the expected number of cod of each 10 cm length class present in various combined sets of clusters, under the hypothesis of no size selectivity in cod feeding (striped bar). Also, the observed number of cod in each length class in the combined sets of clusters (solid bar), with Chi-square goodness-of-fit statistic. For all comparisons, df = 7 $X^2_{0.05,7}=14.07$.

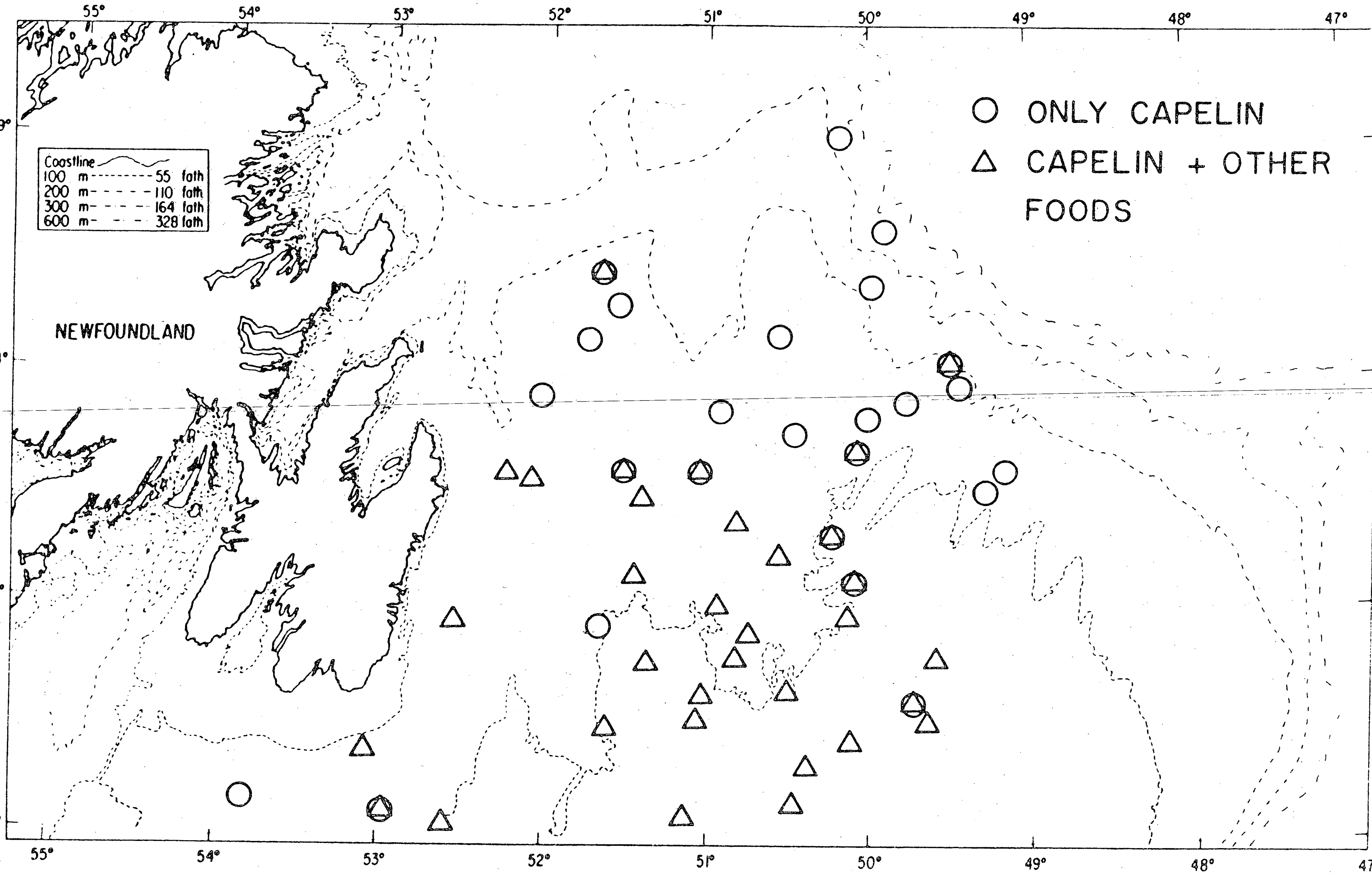

Fig. 15. For stomachs classified as members of clusters defined by feeding on capelin (either exclusively, or in combination with other prey), the positions of sets from which the stomachs were collected.

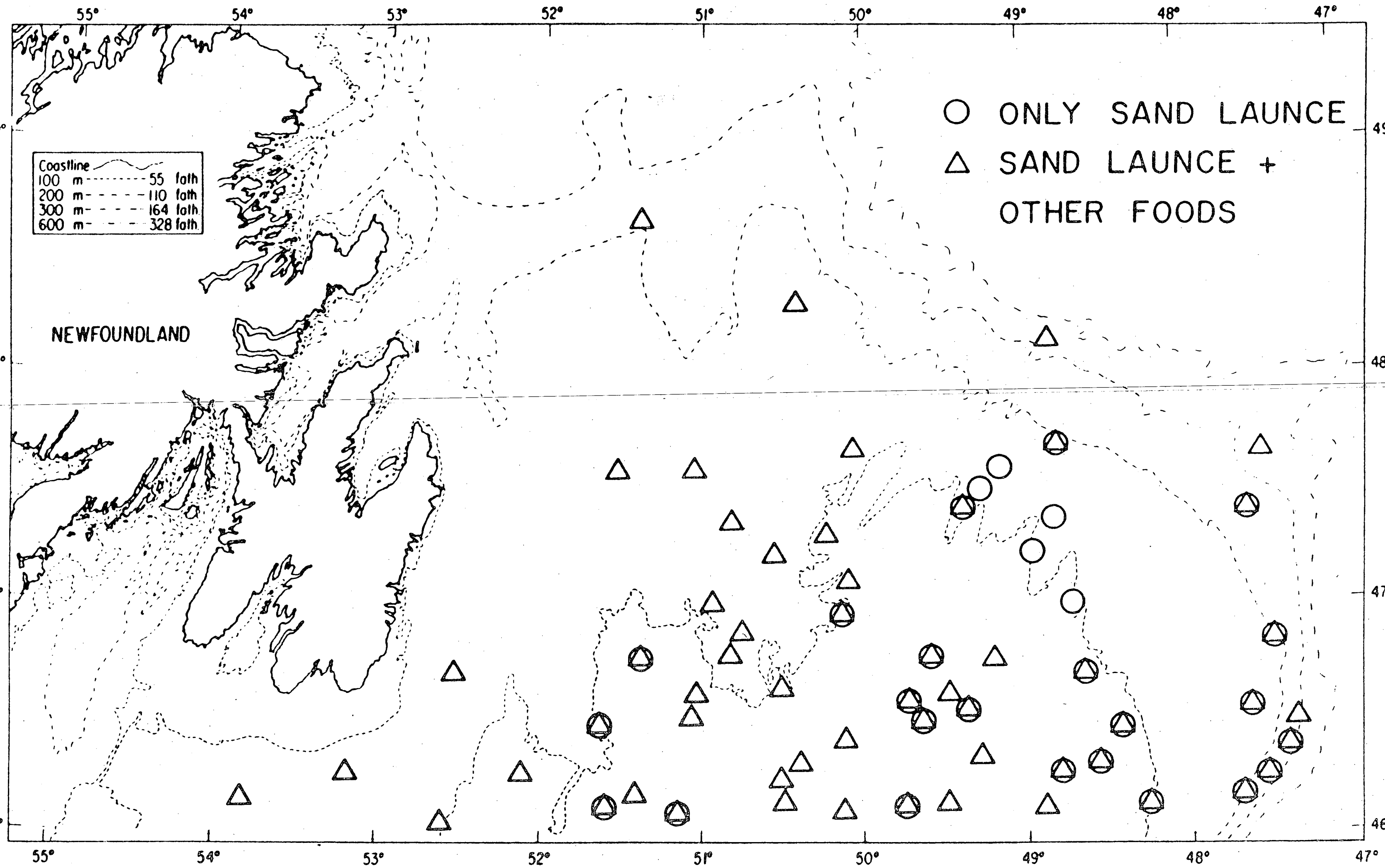

Fig. 16. For stomachs classified as members of clusters defined by feeding on sand lance (either exclusively, or in combination with other prey), the positions of sets from which the stomachs were collected.

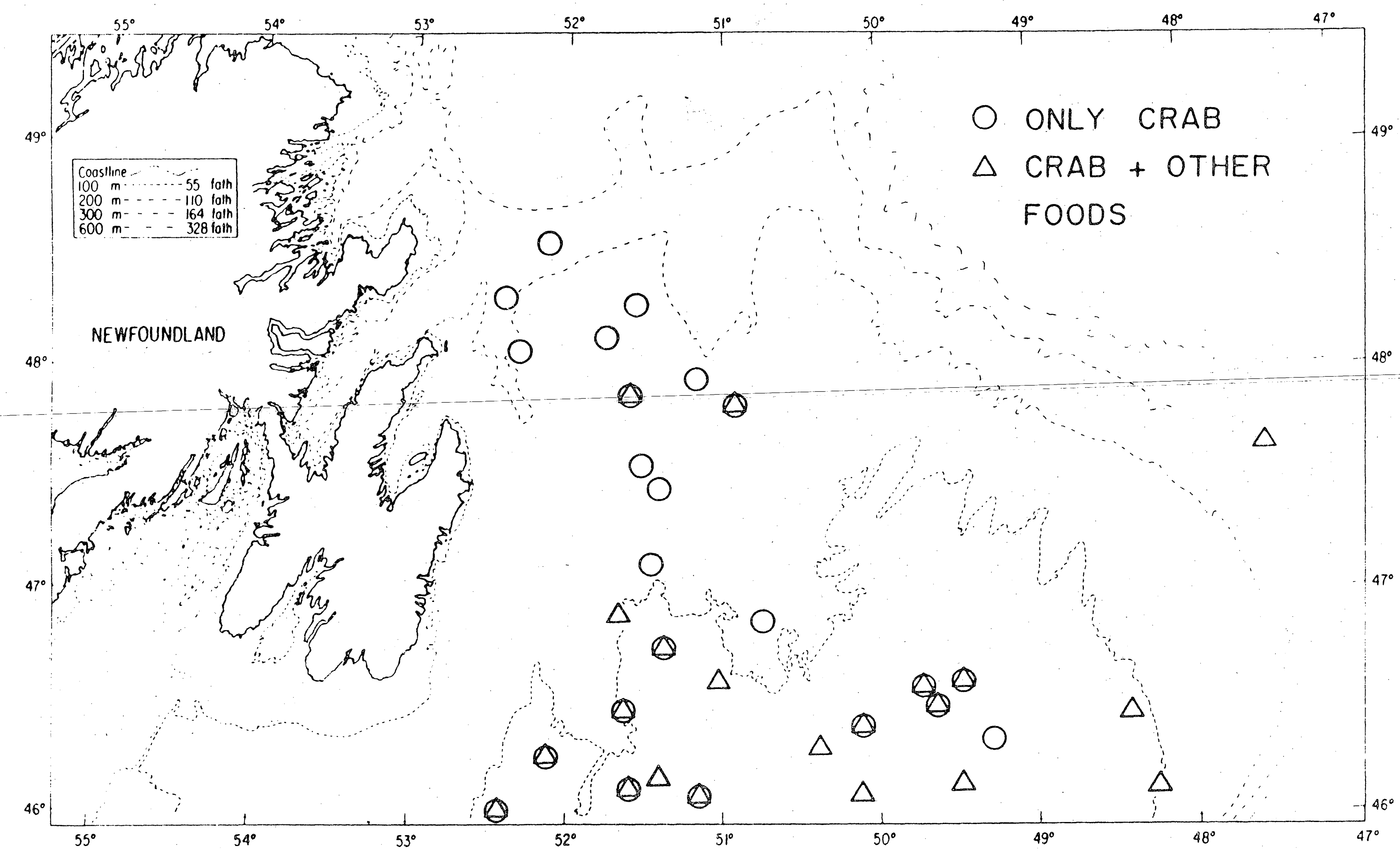

Fig. 17. For stomachs classified as members of clusters defined by feeding on queen crab (either exclusively, or in combination with other prey), the positions of sets from which the stomachs were collected.

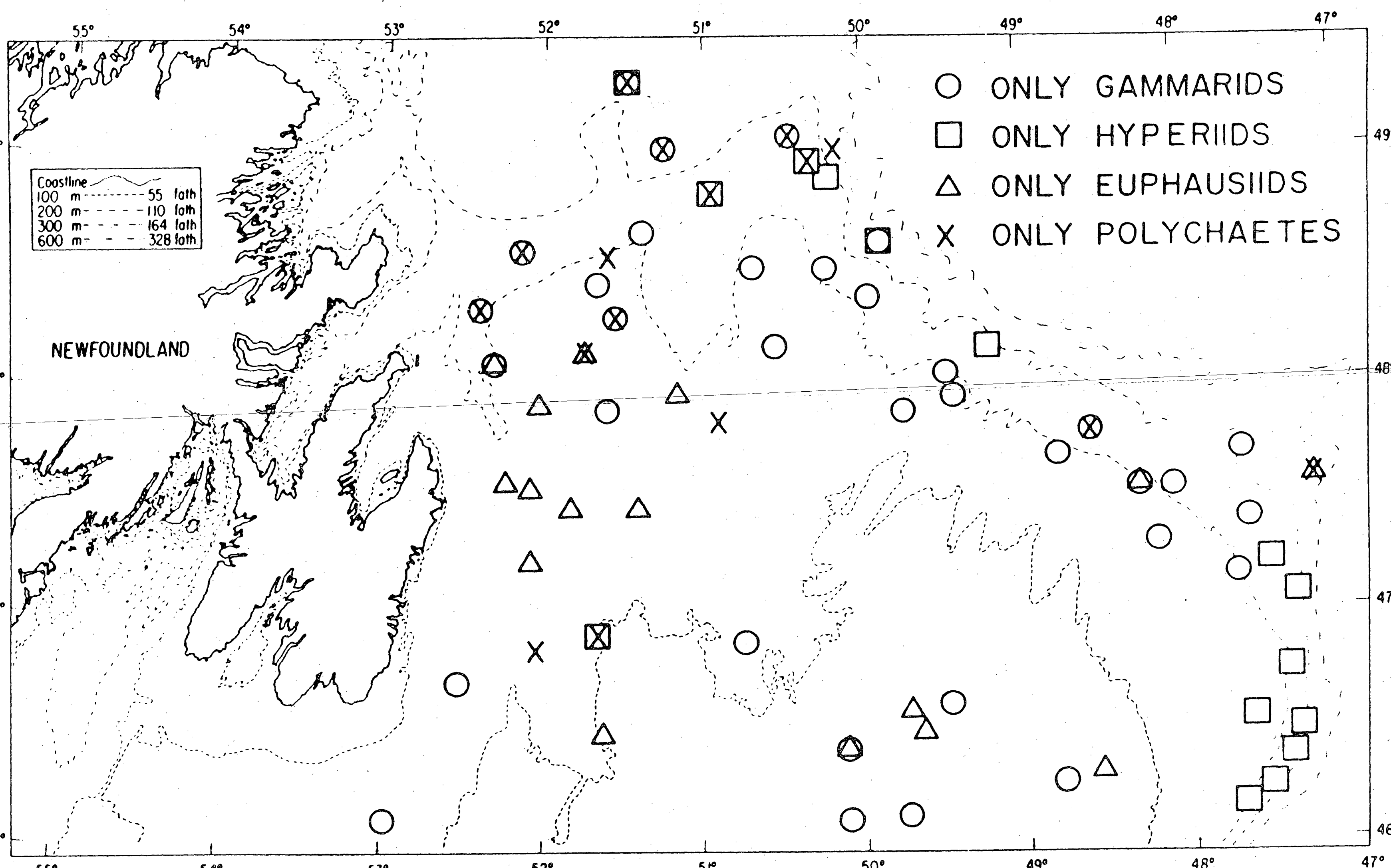

Fig. 18. For stomachs classified as members of clusters defined by feeding exclusively on each of four minor invertebrate prey (gammarids, hyperiids, euphausiids, polychaetes), the positions of sets from which the stomachs were collected.

Appendix 1. Taxa identified in stomachs of cod on the northern Grand Bank, May - June 1979.

	Occurrence Act.	Occurrence PC	Gravimetric Act.	Gravimetric PC	Mean PFI
CLUPEIFORMES	2.	0.11	141.2	0.16	0.003
MALLOTUS VILLOSUS	362.	19.07	13561.4	15.03	0.431
CHAULIODUS SLOANI	6.	0.32	216.6	0.24	0.005
STOMIAS BOA FEROX	12.	0.63	334.5	0.37	0.006
IDIACANTHUS FASCIOLA	1.	0.05	16.8	0.02	0.000
MYCTOPHIDAE	13.	0.68	261.0	0.29	0.007
PARALEPIS SP.	2.	0.11	63.7	0.07	0.002
PARALEPIS BREVIS	1.	0.05	29.2	0.03	0.001
SERRIVOMER BEANI	4.	0.21	212.3	0.24	0.005
GADUS MORHUA	5.	0.26	972.1	1.08	0.006
BOREOGADUS SAIDA	12.	0.63	35.5	0.04	0.001
GAIDROPSARUS ENSIS	1.	0.05	3.0	0.00	0.000
NEZUMIA BAIRDI	2.	0.11	573.8	0.64	0.005
AMMODYTIDAE	376.	19.81	25257.4	28.00	0.738
ANARHICHOIDAE	1.	0.05	0.5	0.00	0.000
STICHAEIDAE	2.	0.11	6.1	0.01	0.000
ULVARIA SUBBIFURCATA	1.	0.05	29.2	0.03	0.001
ZOARCIDAE	5.	0.26	361.3	0.40	0.002
LYCODES SP.	12.	0.63	178.4	0.20	0.003
LYCODES VAHLII	1.	0.05	13.5	0.01	0.000
SEBASTES SP.	5.	0.26	66.9	0.07	0.002
SEBASTES MENTELLA	1.	0.05	213.6	0.24	0.002
COTTIDAE	18.	0.95	112.0	0.12	0.005
ARTEDIELLUS UNCINATUS	1.	0.05	4.7	0.01	0.000
TRIGLOPS SP.	4.	0.21	27.2	0.03	0.002
TRIGLOPS MURRAYI	36.	1.90	370.6	0.41	0.015
TRIGLOPS NYBELINI	1.	0.05	1.9	0.00	0.000
COTTUNCULUS MICROPS	1.	0.05	13.0	0.01	0.000
ICELUS SP.	2.	0.11	8.1	0.01	0.000
ICELUS BICORNIS	1.	0.05	7.1	0.01	0.000
AGONUS DECAGONUS	2.	0.11	38.9	0.04	0.000
ASPIDOPHOROIDES MONOPTERYGIUS	4.	0.21	9.6	0.01	0.000
CYCLOPTERIDAE	1.	0.05	68.6	0.08	0.001
PLEURONECTIFORMES	63.	3.32	1068.9	1.18	0.011
HIPPOGLOSSOIDES PLATESSOIDES	27.	1.42	1954.0	2.17	0.014
LIMANDA FERRUGINEA	1.	0.05	2.5	0.00	0.000
REINHARDTIUS HIPPOGLOSSOIDES	7.	0.37	806.7	0.89	0.009
FISH	310.	16.33	2076.8	2.30	0.059
INVERTEBRATA	50.	2.63	56.9	0.06	0.002
SCYPHOZOA	1.	0.05	10.0	0.01	0.000
ANTHOZOA	10.	0.53	16.2	0.02	0.001
ACTINARIA	33.	1.74	104.7	0.12	0.003
RHYNCHOCOELA	4.	0.21	25.5	0.03	0.001
CHAETOGNATHA	21.	1.11	9.0	0.01	0.000
MOLLUSCA	81.	4.27	171.7	0.19	0.007
GASTROPODA	142.	7.48	455.3	0.50	0.016
THECOSOMATA	8.	0.42	5.2	0.01	0.000
GYMNOSOMATA	1.	0.05	0.2	0.00	0.000
BIVALVIA	12.	0.63	31.7	0.04	0.001

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Appendix 1. (cont.)

CYRTODARIA SILIQUA	1.	0.05	1.0	0.00	0.000
CEPHALOPODA	23.	1.21	509.7	0.57	0.008
SEPIOLIDAE	1.	0.05	11.2	0.01	0.000
OCTOPODA	1.	0.05	89.2	0.10	0.002
ANNELIDA	3.	0.16	0.9	0.00	0.000
POLYCHAETA	[illegible]	27.92	586.9	0.65	0.026
SIPUNCULIDA	10.	0.53	7.1	0.01	0.000
CRUSTACEA	79.	4.16	80.9	0.09	0.003
COPEPODA	19.	1.00	2.0	0.00	0.000
CUMACEA	12.	0.63	12.2	0.01	0.001
TANAIDACEA	4.	0.21	0.4	0.00	0.000
ISOPODA	100.	5.27	179.2	0.20	0.009
AMPHIPODA	3.	0.16	0.7	0.00	0.000
HYPERIIDAE	345.	18.18	1196.7	1.33	0.053
GAMMARIDEA	822.	43.31	1472.0	1.63	0.061
CAPRELLIDEA	11.	0.58	5.6	0.01	0.000
MYSIDACEA	13.	0.68	1.5	0.00	0.000
ERYTHROPS SP.	1.	0.05	0.1	0.00	0.000
ERYTHROPS ERYTHROPHTHALMA	44.	2.32	4.5	0.00	0.000
METERYTHROPS ROBUSTA	1.	0.05	0.1	0.00	0.000
EUPHAUSIACEA	427.	22.50	5513.7	6.11	0.175
MEGANYCTIPHANES NORVEGICA	6.	0.32	3.1	0.00	0.000
THYSANOESSA INERMIS	4.	0.21	1.8	0.00	0.000
THYSANOESSA RASCHI	257.	13.54	2703.2	3.00	0.091
THYSANOPODA SP.	1.	0.05	10.5	0.01	0.000
THYSANOPODA ACUTIFRONS	1.	0.05	5.1	0.01	0.000
NATANTIA	151.	7.96	180.7	0.20	0.008
GENNADAS ELEGANS	16.	0.84	120.5	0.13	0.003
ACANTHEPHYRA PELAGICA	1.	0.05	14.0	0.02	0.000
PASIPHAEA SP.	3.	0.16	15.2	0.02	0.000
HIPPOLYTIDAE	13.	0.68	13.5	0.01	0.000
EUALUS SP.	18.	0.95	5.2	0.01	0.000
EUALUS FABRICII	1.	0.05	0.7	0.00	0.000
EUALUS PUSIOLUS	2.	0.11	0.3	0.00	0.000
EUALUS MACILENTUS	62.	3.27	29.8	0.03	0.001
EUALUS STONEYI	1.	0.05	0.2	0.00	0.000
EUALUS GAIMARDII	26.	1.37	25.8	0.03	0.002
SPIRONTOCARIS SP.	4.	0.21	5.9	0.01	0.000
SPIRONTOCARIS SPINUS	69.	3.64	86.3	0.10	0.005
SPIRONTOCARIS PHIPPSI	12.	0.63	6.9	0.01	0.001
SPIRONTOCARIS LILLJEBORGI	4.	0.21	0.8	0.00	0.000
LEBBEUS SP.	2.	0.11	2.4	0.00	0.000
LEBBEUS GROENLANDICUS	1.	0.05	25.1	0.03	0.000
LEBBEUS POLARIS	35.	1.84	54.1	0.06	0.002
PANDALUS SP.	43.	2.27	147.1	0.16	0.007
PANDALUS BOREALIS	61.	3.21	94.6	0.10	0.003
PANDALUS MONTAGUI	179.	9.43	1274.1	1.41	0.044
CRANGONIDAE	4.	0.21	16.3	0.02	0.000
SABINEA SEPTEMCARINATA	16.	0.84	46.3	0.05	0.002
SABINEA SARSI	2.	0.11	1.5	0.00	0.000
ARGIS DENTATA	7.	0.37	27.7	0.03	0.001
REPTANTIA	131.	6.90	1397.9	1.55	0.035
PAGURIDAE	16.	0.84	42.2	0.05	0.001
PAGURUS SP.	20.	1.05	66.7	0.07	0.002
PAGURUS LONGICARPUS	1.	0.05	1.0	0.00	0.000
MAJIDAE	1.	0.05	0.1	0.00	0.000
CHIONOECETES OPILIO	257.	13.54	12928.1	14.33	0.262
HYAS SP.	102.	5.37	3834.5	4.25	0.081
HYAS ARANEUS	113.	5.95	5387.2	5.97	0.123
HYAS COARCTATUS	40.	2.11	677.8	0.75	0.012
HOLOTHUROIDEA	18.	0.95	104.3	0.12	0.002
ECHINOIDEA	1.	0.05	0.3	0.00	0.000
ASTEROIDEA	1.	0.05	0.2	0.00	0.000
OPHIUROIDEA	47.	2.48	66.9	0.07	0.002
ASCIDACEA	67.	3.53	1051.6	1.17	0.026
LARVACEA	1.	0.05	0.7	0.00	0.000
UNID.	58.	3.06	73.4	0.08	0.003
PLANT	1.	0.05	0.1	0.00	0.000
			90199.6		