RESTRICTED

International Commission for the Northwest Atlantic Fisheries

Serial No. 3967
(D.c.9)

ICNAF Res.Doc. 76/VI/121

ANNUAL MEETING - JUNE 1976

A preliminary analysis of inter-specific trophic relationships between the sea herring, *Clupea harengus* Linnaeus and the Atlantic mackerel, *Scomber scombrus* Linnaeus.

by

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The Atlantic sea herring (*Clupea harengus*) and the Atlantic mackerel (*Scomber scombrus*) share many common characteristics, i.e., distribution, abundance, and size. Ecologically, they can be described as pelagic, schooling and fast swimming zooplankton feeders associated with similar water masses along the continental shelf of the northeast coast of the United States from Cape Hatteras, ranging in winter to boreal waters. Morphologically both species are laterally compressed and possess pronounced visual acuity. Their general feeding strategies are also alike as either can select prey items or "filter feed". With so many similar niche parameters a measurable degree of overlap between food resources might be expected. Previous works have listed the food items which dominate the diets of both species. Over the area of investigation, the herring have been reported as feeding on small copepods (Saunders, 1952), large copepods (Pavshtics, 1965), copepods, euphausiid shrimp and amphipods (Paulmier and De Camps, 1973) and chaetognaths, copepods and euphausiid shrimp (Maurer and Bowman, 1975). Sette (1943) first linked mackerel to *Calanus* rich waters, while others have reported the dominance of chaetognaths, small copepods and pteropods (Maurer and Bowman, 1975).

Mackerel and herring constitute a valuable international resource off the USA and Canadian coasts. In 1973 foreign and domestic fisheries removed 4.16×10^5 MT of herring and 4.67×10^5 MT of mackerel from ICNAF Subareas 4, 5, and 6 (regions, Southern New England, Georges Bank, and the Gulf of Maine). The combined effects of increased effort and gear efficiency have contributed to a reduction of fishable stocks and recruitment of both species. Focus must be placed on trophic relationships, which may determine population structure and be a significant factor in determining the ability of each stock to recover.

In the spring of 1974 the Northeast Fisheries Center, Woods Hole initiated a special preliminary study designed to investigate the similarities and measure the overlap, of the food habits of herring and mackerel.

Methods

Herring and mackerel were collected at preselected survey stations with a Yankee "36" otter trawl, constructed with a 2-inch mesh body with a 3/4-inch cod end liner. The vertical opening of this trawl averages approximately eight feet. Towing times were standardized at 30 minutes and towing speed at three knots. Although samples were collected from the Middle Atlantic to the Nova Scotian Shelf, sampling was concentrated in the areas of Southern New England and Georges Bank (Figure 1).

To guarantee preservation of stomach contents the body cavity was slit and a small amount of 10% formalin was injected directly into the stomach before storing in plastic containers.

In the laboratory, the fish were measured to the nearest millimeter (fork length) and grouped by sex and size. Thus, the stomach contents from all fish of the same sex and size group collected at a single station were pooled. Food items were identified to the lowest taxa possible and counted. Each fraction was damp dried and weighed to an accuracy of $\pm$ .001 grams. Items weighing less than .001 gram were recorded as trace.

In order to reduce the variability associated with wet weights of small individual items or small groups of plankters (i.e., copepods, amphipods, etc.), large numbers of the more frequent food items were weighed and a mean weight per specific item was then used as a conversion factor for that particular item and for organisms of similar size and morphology.

When the pooled sample volume exceeded 10 milliliters it was reduced to a manageable size using a modified Motoda plankton splitter (Marine Research, Inc.). At one particular station (Sta. 6) where the diet of both species was more or less monotypic, size seiving proved to be an effective means of separating the numerically dominant larger food type (*Limacina retroversa*, mackerel; *Sagitta elegans*, herring) from the smaller,less numerous forms (*Centropages, Pseudocalanus*, barnacle cypris).

Size classes (Table 1) were established for both predators. Mackerel length groups were determined after examination of length frequency modes of mackerel taken from all stations on this survey. Length groups of herring were established after analysis of size frequency modes of commercial landings for spring 1973 as compared with spring 1974. The majority of fish were taken from different size groups within species (see Table 2; herring, 90% from size group 4; mackerel, 54% from size group 1). However, the actual size of these fish overlap between species, 22.0-26.9 mm and 16.0-24.9 mm, respectively (Table 1)

Results and Discussion

General characteristics of herring diet

A complete list of food items eaten by herring is presented in Table 3. A total of 32 different prey items was identified.

Examining the general quantitative composition by weight and number, clearly, chaetognaths dominated the diet by weight (43%) and number (68%). All chaetognaths were identified as *Sagitta elegans*, a common carnivorous zooplankter averaging 20 mm in length, especially abundant in the area of Georges Bank where densities of 5,840 per 100 cubic meters have been reported (Clarke et al., 1943). Euphausiids as a group accounted for 34% of the stomach content weight, however, only 0.6% of the numbers. Euphausiids were one of the largest prey items ingested by herring, approximately 40 mm in length, constitute an extremely important prey resource in the outer shelf and slope waters. These shrimp-like crustaceans are known to perform diel vertical migrations, a behavior which may account for their importance in the food chains of many demersal as well as pelagic predators. Of the two species identified, *Meganyctiphanes norvegica* was the dominant form in terms of diet weight, 23.1%, while *Thysanoessa inermis* represented 6.1% of the diet weight. The shelled pteropod, *Limacina retroversa*, ranks third in importance as regards diet weight (6.2%) and numbers (10.6%). Common in coastal waters, Bigelow (1926) reports swarming (extremely high local densities) occurs seasonally in the vicinity of Georges Bank and the Gulf of Maine. Individuals usually range in size from 1-2 mm in diameter. As an aggregate, copepods represented only 3% of the diet weight and 8% of the diet numbers. Twelve genera were identified, ten calanoid, one cyclopoid (*Oithona*) and one harpacticoid (*Macrosetella*). In order of numerical importance the four dominant copepod genera are: *Calanus finmarchicus, Centropages typicus, Pseudocalanus minutus,* and *Candacia armata.* All are common coastal shelf-water species ranging in size (length) from 0.5 mm to 1.2 mm. Barnacle cypris (larval stages) made up 12.2% of diet numbers while contributing only 0.6% to diet weight. This meroplankton component is a seasonal (spring-summer) member of the plankton and is known to occur in local patches resulting from simultaneous release of nauplii by adults. The mean size of these larvae was

0.5 mm. Larval and juvenile fish comprised only 0.4% of the diet weight. The most frequently occurring were sand lance, *Ammodytes americanus*, and a singular occurrence of cannibalism, one herring larvae.

The remainder of the food groups reported contribute a rather insignificant amount to diet weight or numbers. These include larvaceans, pandalid shrimp, gammarid and hyperiid amphipods. The presence of demersal crustaceans, five pandalids, fifteen gammarid amphipods, and a few sand grains indicate occasional departures from the pelagic feeding habit.

General characteristics of mackerel diet

A total of 38 different food items was identified (Table 3). Copepods (32.7%) and pteropods (33.5%) contributed almost equally to the diet weight. However, their numbers were quite disproportionate, the smaller copepods constituting 81.5% of the diet numbers. All pteropods were *L. retroversa* except thirteen gynmosomate forms of the genus *Clione*. Nine copepod genera were identified, although only four genera dominated weight and numbers; their numbers ranging from 2-3 orders of magnitude above the other copepod genera. In order of dominance by weight and numbers they are *C. typicus, P. minutus, Temora longicornis,* and *C. finmarchicus*. Other calanoid genera, cyclopoid and harpacticoid copepods occurred in relatively small numbers and as a group made up only about 1% of the diet weight. Larvaceans comprised 5.1% of diet weight and 2% of diet numbers; clearly dominated by the small coastal form *Oikopleura dioca,* size range 1-1.5 mm. Some 18 larval and post-larval fish represented 4.5% of the diet weight. Although fish eggs did not contribute much to diet weight (0.4%), a total of 68 were enumerated. Euphausiids, *M. norvegica* (4.1%) and *T. inermis* (0.1%) occurred in the same relative proportion as in the herring diet.

Decapods were of little importance, 3.4% of the diet weight. Larger adult forms were ingested in small numbers; *Crangon* (20), *Pandalus* (3), Sergestid shrimp (1), while smaller pelagic larvae were taken in substantially greater numbers; decapod larvae (749) and *Pagurus zoea* (6).

Other minor foods include *Neomysis* (0.5% diet weight), *Ophiura* (0.2%), hyperiid amphipods (0.2%), gastropod veliger, pelecypod veliger, cumaceans, gammarid amphipods, polychaete larvae, and siphonophores.

An ecological classification of food types

The foods listed in Table 3 cover a broad phylogenetic spectra from unicellular forms (diatoms and foraminifera) to fish. However, if the different foods are classified on an ecological basis according to life form (Odum, 1971), they can be grouped as one of three ecological types; holoplanktonic, meroplanktonic, or epibenthic (Table 4).

Both herring and mackerel depend almost entirely on the holoplanktonic component for their food supply. True planktonic forms constituted 98.9% of the weight of food organisms consumed by herring and 95.2% of those consumed by mackerel. Although the planktonic larval stages of certain benthic invertebrates (barnacle cypris and decapod larvae) were consumed by both species in substantial numbers, these items contributed only about 1% to the total stomach content weight. Therefore the meroplankton component did not constitute a significant source of energy for these pelagic feeders during this survey. The epibenthic component can be considered as a third potential food source. Epibenthic crustaceans (*Neomysis* and *Crangon*) contributed 3.8% to the mackerel stomach content weight and only 0.2% of the herring stomach content weight. If we were to consider the epibenthos as a serious alternative resource for either species, mackerel would seem to be slightly more successful in foraging for epibenthic forms than herring, thus able to supplement its diet when suitable plankton is scarce.

Prey size and biomass

The relative trophic requirements, as regards prey size and biomass, can be determined if we compare the mean weight and mean number ratio of prey per stomach for each species:

$$\text{Biomass ratio} = \frac{\bar{x}\ \text{weight mackerel stomach contents}}{\bar{x}\ \text{weight herring stomach contents}}$$

$$= 1.61$$

$$\text{Number ratio} = \frac{\bar{x}\ \text{number mackerel food items}}{\bar{x}\ \text{number herring food items}}$$

$$= 5187$$

Considering only fish with stomachs containing food, the average prey biomass for mackerel was 0.742 g and 0.461 g for herring which results in a biomass ratio of 1.61.

The number ratio, 5.87, indicates that mackerel are ingesting 5.87 times as many prey items as herring. Referring to Table 3 the ratio is the result of mackerel consuming large numbers of small calanoid copepods especially *Pseudocalanus minutus*, *Centropages typicus*, and *Temora longicornis*.

A general conclusion would be that mackerel feed on a larger number of smaller prey items than does herring.

A measure of competition potential

A further analysis of the total diet examines the potential for competition. The generic items from Table 3 are arranged in Table 5 to show the prey genera which occurred in diets of both herring and mackerel. These can be considered as items over which competition may result. Sixteen of the 29 food organisms identified to the generic level were consumed by both species. These include two amphipods, *Meganyctiphanes* and *Neomysis;* ten copepod genera, *Limacina, Sagitta, Oikopleura,* and *Ammodytes.* All of the items which contribute significantly to the stomach content weight (Table 3) co-occur.

Analysis of diet similarity and food overlap

This section considers only those eleven stations where herring and mackerel were collected together (Figure 1).

In order to perform the following analysis, the individual food items were grouped; e.g., copepods and amphipods. Only a minimal loss in the ability to identify specific prey items occurred because of the strong dominance within groups by only one or two species, except copepods where three or four genera shared dominance.

First the relative importance of the prey groups within the co-occurring subset of stations was established using the Index of Importance (I.I.) first proposed by Bogorov (1934). This index is similar to one recently used by Hobson (1974) to rank the food items of reef fishes. The importance of a given food component is expressed jointly on the basis of weight (percent weight) and how common the item is in the diet of the species examined (percent occurrence). These data are combined in the following manner:

$$\text{I.I.} = \sqrt{(\%\ \text{weight})\ (\%\ \text{occurrence})}$$

A comparison of indices for a number of food organisms characterizes the importance of that particular food item to that species of fish.

The calculated indices appear in Table 6. Herring prey groups, ranked in order of decreasing importance, are 1) chaetognaths (53.6), 2) euphausiids (20.3), 3) pteropods (18.0), and 4) copepods (13.1). The other prey groups were less important, I.I. ranging from 0 to 0.7. Of the ten prey groups considered only two are of substantial importance in the mackerel diet, copepods (53.1) and pteropods (39.7).

Groups of lesser importance include fish (7.3), larvaceans (5.3), chaetognaths (3.9), amphipods (2.3), mysids (2.3), echinoderms (2.1), euphausiids (1.4), and barnacle cypris (<0.1). Note that the food groups that rank one (copepods) and two (pteropods) in the mackerel diet, rank third and fourth in the herring diet.

Having established the relative importance of food groups within species, the diet similarities between herring and mackerel were analyzed following two different methods. Yanulov (1963) introduced a simple proportion called the Coefficient of Food Similarity (CFS), which he used to compare patterns of feeding in redfish (*Sebastes mentella*). In 1972, Vinogradov applied the same formula to measure feeding similarity between silver and red hake. This formula is stated as follows:

$$\text{Coefficient of Food Similarity (CFS)} = \frac{n \times 100}{N}$$

N = sum of the higher percentages of occurrence of food organisms for compared species.

n = sum of the lower percentages of occurrence of food organisms for compared species.

The CFS can range from 0, no similarity, to 100 indicating complete similarity. This index, as used in the past, has only been applied to frequency of occurrence data.

The second method, introduced by Morisita (1959), was developed as an objective tool for ecologists to measure overlap between species. Pearcy and Ambler (1974) used a modification of Morisita's index (Horn, 1966) known as C_λ , to compare food habits of deep-sea macrourid fishes.

$$C_\lambda = \frac{\sum_{i=1}^{s} X_i Y_i}{\sum_{i=1}^{s} X_i^2 + \sum_{i=1}^{s} Y_i^2}$$

s = total number of food groups in both samples, and food group i is represented proportionally x_i percent in the herring diet and y_i percent in the mackerel diet.

The index ranges from 0, no overlap, to 1.0, complete overlap. This measure is preferred by many because of its increased sensitivity to varying proportional compositions of the samples being compared.

Both measures, CFS and C_λ, were calculated for frequency of occurrence and percent weight using the data groups in Table 6. Horn's 1966 formula, C_λ when used to compare frequency of occurrence of different taxa indicated a high amount of overlap (0.82). However, the C_λ overlap was small (0.12) when based on the percent weight of the different taxa. The rather large difference in diet overlap when calculated on a percent occurrence and percent weight basis is explained by the fact that although the frequency of occurrence of some items (copepods, 91%; *L. retroversa*, 43.2%) in the herring diet is quite high, their numbers are relatively low and only account for 1.9% and 7.5% of the diet weight, respectively. In addition, chaetognaths which occur in similar frequency in both diets (44.4% and 30%) dominate the herring diet weight 64.8%, however, only account for 0.5% of the mackerel diet weight. Yanulov's 1963 measure, CFS, indicates a somewhat less significant (43.6) similarity based on percent occurrence and a 7.4 value calculated for percent weight. In general, these measures indicate that both species often feed on the same types of prey, although the proportions of specific items frequently vary significantly between species.

How do the calculated values compare to the results of other investigators? Pearcy and Ambler (1974) reported overlap C_λ values, of 0.86 (percent occurrence) and 0.04 (percent weight) between two congeneric macrouid species. As in the present investigation, those items which occurred with similar frequency in both diets did not necessarily account for similar proportions of the diet weight. Vinogradov (1972), considering percent occurrence, reported a similarity, CFS value of 30.8, comparing the diets of red and silver hake which he judged to be not serious. Diet similarity calculated in this report, 43.6, is somewhat higher, however, does not approach the significance of a C_λ value of 0.82. Therefore the degree of similarity or overlap is not only dependent upon which stomach analysis parameter we choose to test, percent occurrence or percent weight, but can be effected by the choice of index, CFS or C_λ. A measure of similarity or overlap based on the frequency of occurrence of food items does not consider the relative proportions of food items in the diet.

Investigations of possible competition should only be based on quantitative measures (percent weight or percent volume). Further analysis of the two indexes shall be required to determine the relative levels of significance for each before they can be used with confidence in feeding studies.

The degree of overlap appears to be influenced by relatively few species which occur in the diet. These "key" species are listed in Figure 2. Analysis of Figure 2 suggests that the high index variability in the Southern New England region is due to the selective nature of feeding on two zooplankton organisms, *Limacina retroversa* and *Sagitta elegans*. Index values range from a high of 0.98, both diets dominated by *L. retroversa* to a low of 0.098, mackerel again feeding on the pteropod however, in marked contrast over 90% of the herring diet consisting of *S. elegans*. The consistently high overlap values on Georges Bank can be explained by the fact that both species were feeding on the "krill shrimp", *Meganyctiphanes norvegica*. It has been established that zooplankton diversity is greatest in equatorial waters decreasing continually from south to north. Following that rational, food similarity should increase, proceeding northward from the mid-Atlantic to the Scotian Shelf, as the number of available prey types is reduced. Hence the production of fish species will become more species specific as we proceed toward boreal waters. In general, Figure 2 tends to support this hypothesis, the extent of overlap in the mid-Atlantic being dependent upon a mixed group of numerous small calanoid copepods, in the Southern New England are being dependent on two zooplankton species and on Georges Bank being specific to only one genera, *Meganyctiphanes norvegica*.

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Table 1. Size groups established for herring and mackerel from the analysis of length frequency modes; fork length in millimeters.

	Size group				
	1	2	3	4	5+
Sea herring	---	9.0-15.9	16.0-21.9	22.0-26.9	>27.0
Mackerel	16.0-24.9	25.0-28.9	29.0-32.9	(4+) >33.0	---

Table 2. Size distribution of herring and mackerel analyzed for this investigation.

	HERRING		MACKEREL	
	Number examined		Number examined	
Size group	All stations	Co-occurring stations	All stations	Co-occurring stations
1	0	0	139	93
2	12	2	58	31
3	2	2	24	17
4	185	82	38	27
5	5	5	4+	
Total examined	204	91	259	168

Table 3. A list of food items resulting from the quantitative analysis of stomach contents of all mackerel and herring sampled. Weight (wet weight) expressed in grams.

Prey items	Atlantic mackerel				Sea herring			
	Weight		Number		Weight		Number	
	g	% of Total	No.	% of Total	g	% of Total	No.	% of Total
FORAMINIFERA	Tr	<0.1	2	<0.1	-	-	-	-
DIATOMS	-	-	- -	-	.034	<0.1	7	<0.1
SIPHONOPHORE	.011	0.1	2	<0.1	-	-	-	-
HYDROZOA	Tr	-	-	-	.053	<0.1	4	<0.1
POLYCHAETE LARVAE	.002	<0.1	11	<0.1	.001	<0.1	4	<0.1
AMPHIPODA								
Gammaridea	.015	<0.1	5	<0.1	.081	0.1	13	<0.1
Gammarus	.062	<0.1	6	<0.1	.010	<0.1	2	<0.1
Hyperidea	.002	<0.1	1	<0.1	.022	<0.1	3	<0.1
Hyperia	.357	0.2	97	<0.1	.029	<0.1	9	<0.1
Hyperiid	.028	<0.1	7	<0.1	-	-	-	-
DECAPODA								
Crangon	2.656	1.8	20	<0.1	-	-	-	-
Pagurus zoea	.056	<0.1	6	<0.1	.023	<0.1	9	<0.1
Pandalidae	-	-	-	-	.020	<0.1	5	<0.1
Pandalus	1.334	0.9	3	<0.1	-	-	-	-
Sergestidae	.099	<0.1	1	<0.1	-	-	-	-
Decapod larvae	.814	0.5	749	0.3	.131	<0.1	85	0.2
ISOPODA	-	-	-	-	.010	<0.1	12	<0.1
CUMACEA								
Diastylus	.014	<0.1	10	<0.1	.003	<0.1	1	<0.1
EUPHAUSIACEA								
Meganyctophanes norvegica	6.128	4.1	51	<0.1	18.627	23.1	133	0.3
Thysanoessa inermis	.419	0.1	28	<0.1	4.886	6.1	103	0.2
Other euphausiids	-	-	-	< -	3.057	3.8	32	<0.1
MYSIDACEA								
Neomysis	.738	0.5	134	<0.1	.007	<0.1	3	<0.1
Other mysids	-	-	-	-	.003	<0.1	4	<0.1
CIRRIPEDEA (Cypris)	Tr	<0.1	5	<0.1	.501	0.6	5,131	12.2

Table 3. cont'd

	Atlantic mackerel				Sea herring			
	Weight		Number		Weight		Number	
	g	% of Total	No.	% of Total	g	% of Total	No.	% of Total
COPEPODA								
Calanus finmarchicus	3.828	2.6	3,399	1.2	1.568	1.9	1,459	3.5
Calanus	-	-	-	-	.003	<0.1	36	0.1
Calanidae	-	-	-	-	Tr	<0.1	2	<0.1
Rhincalanus nasutus	.015	<0.1	15	<0.1	.012	<0.1	14	<0.1
Centropages typicus	12.969	8.8	58,491	21.0	.195	0.2	824	1.9
Temora longicornis	9.135	6.2	40,144	14.4	.005	<0.1	50	0.1
Pseudocalanus minutus	10.206	6.9	51,222	18.4	.050	<0.1	277	0.6
Euchirella rostrata	-	-	-	-	Tr	<0.1	1	<0.1
Metridia lucens	.012	<0.1	17	<0.1	.013	<0.1	41	0.1
Pleuromamma	.015	<0.1	18	<0.1	.004	<0.1	8	<0.1
Candacia armata	.017	<0.1	22	<0.1	.080	0.1	134	0.3
Tortanus	-	-	-	-	.001	<0.1	5	<0.1
Calanoid nauplii	Tr	<0.1	1	<0.1	-	-	-	-
Other calanoids	12.202	8.2	73,993	26.5	.128	0.2	479	1.1
Oithona	Tr	<0.1	32	<0.1	Tr	<0.1	7	<0.1
Other cyclopoids	-	-	-	-	Tr	<0.1	1	<0.1
Macrosetella	-	-	-	-	.001	<0.1	4	<0.1
Other harpacticoids	.006	<0.1	49	<0.1	Tr	<0.1	1	<0.1
CRUSTACEAN EGGS	Tr	<0.1	30	<0.1	-	-	-	-
CRUSTACEAN LARVAE	-	-	-	-	.004	<0.1	10	<0.1
PELECYPOD VELIGER	..004	<0.1	3	<0.1	-	-	-	-

Table 3. cont'd

	Atlantic mackerel				Sea herring			
	Weight		Number		Weight		Number	
	g	% of Total	No.	% of Total	g	% of Total	NO.	% of Total
PTEROPODA								
Clione	.059	<0.1	13	<0.1	-	-	-	-
Limacina retroversa	49.507	33.5	43,348	15.6	5.020	6.2	4,478	10.6
GASTROPODA (Veliger)	.035	<0.1	1	<0.1	-	-	-	-
CEPHALOPODA	.209	0.1	1	<0.1	-	-	-	-
ECHINODERMATA								
Ophiura (larvae)	.299	0.2	125	<0.1	-	-	-	-
CHAETOGNATHA								
Sagitta elegans	.704	0.5	647	0.2	34.743	43.[illegible]	28,622	67.9
APPENDICULARIA								
Oikopleura	6.783	4.6	5,606	2.0	.095	0.1	82	0.2
Fritillaria	.758	0.5	244	<0.1	-	-		
TUNICATA	-	-	-	-	Tr	<0.1	1	<0.1
PISCES								
Leptocephalus	.058	<0.1	1	<0.1	-	-	-	-
Urophycis	2.747	1.8	1	<0.1	-	-	-	-
Ammodytes americanus	2.283	1.5	16	<0.1	.351	0.4	4	<0.1
Clupea harengus	-	-	-	-	.015	<0.1	1	<0.1
Unidentified fish	1.763	1.2	1	<0.1	.032	<0.1	14	<0.1
Scales	.004	<0.1	95	<0.1	Tr	<0.1	13	<0.1
Eggs	.625	0.4	68	<0.1	Tr	<0.1	13	<0.1
ANIMAL REMAINS	18.511	12.5			10.324	12.8		
SAND	.002	<0.1			.006	<0.1		
Total weight and number	145.491 g		278,741		80.148 g		42,140	
Number of stomachs with food	196				174			
Mean weight and number	.742 g.		1.422		.461 g.		242	

Table 4. A classification of food groups showing the relative importance of each component in the diet of herring and mackerel.

	ECOLOGICAL TYPES		
	Holoplankton	Meroplankton	Epibenthos
	Foraminifera Diatoms Siphonophores Hyperiid amphipods Sergestid shrimp Euphausiid shrimp Copepods Pteropods Cephalopods Chaetognaths Larvaceans Tunicates Fish	Decapod larvae Barnacle cypris Pelecypod veliger Ophiuroid larvae	Gammarid amphipods *Crangon* Pandalid shrimp Isopods Cumaceans Mysid shrimp
Herring			
Percent diet weight	98.9	0.9	0.2
Number of food types	30	5	3
Mackerel			
Percent diet weight	95.2	1.0	3.8
Number of food types	33	6	5

Table 5. Co-occurring generic food items.

Genera	Herring	Mackerel
Gammarus	+	+
Hyperia	+	+
Diastylus	+	-
Crangon	-	+
Pagurus	-	+
Pandalus	-	+
Meganyctiphanes	+	+
Thysanoessa	-	+
Neomysis	+	+
Calanus	+	+
Centropages	+	+
Temora	+	+
Rhincalanus	+	+
Pseudocalanus	+	+
Euchirella	+	-
Metridia	+	+
Pleuromamma	+	+
Candacia	+	+
Tortanus	+	-
Oithona	+	+
Macrosetella	+	-
Clione	-	+
Limacina	+	+
Sagitta	+	+
Ophiura	-	+
Oikopleura	+	+
Fritillaria	-	-
Merluccius	-	+
Ammodytes	+	+

16/29 co-occurring genera

Table 6. Importance of principle prey groups in the diets of herring and mackerel collected from co-occurring stations.

	Herring			Mackerel		
	% Occurrence	% Weight	I.I.	% Occurrence	% Weight	I.I.
Amphipods	4.9	<0.1	0.7	21.5	0.2	2.3
Copepods	91.0	1.9	13.1	72.9	38.8	53.1
Mysids	0.7	<0.1	<0.1	9.0	0.6	2.3
Euphausiids	16.0	25.7	20.3	0.7	2.8	1.4
Barnacle cypris	11.1	<0.1	<0.1	1.4	<0.1	<0.1
Mollusca	43.2	7.5	18.0	39.6	39.9	39.7
Echinoderms	-	-	-	18.0	0.2	2.1
Chaetognaths	44.4	64.8	53.6	30.0	0.5	3.9
Larvaceans	-	-	-	35.4	0.8	5.3
Fish	1.2	<0.1	<0.1	17.3	3.1	7.3
Coefficient of Food Similarity, CFS			43.6	7.4		
Overlap Index, $\hat{C}$			0.82	0.12		

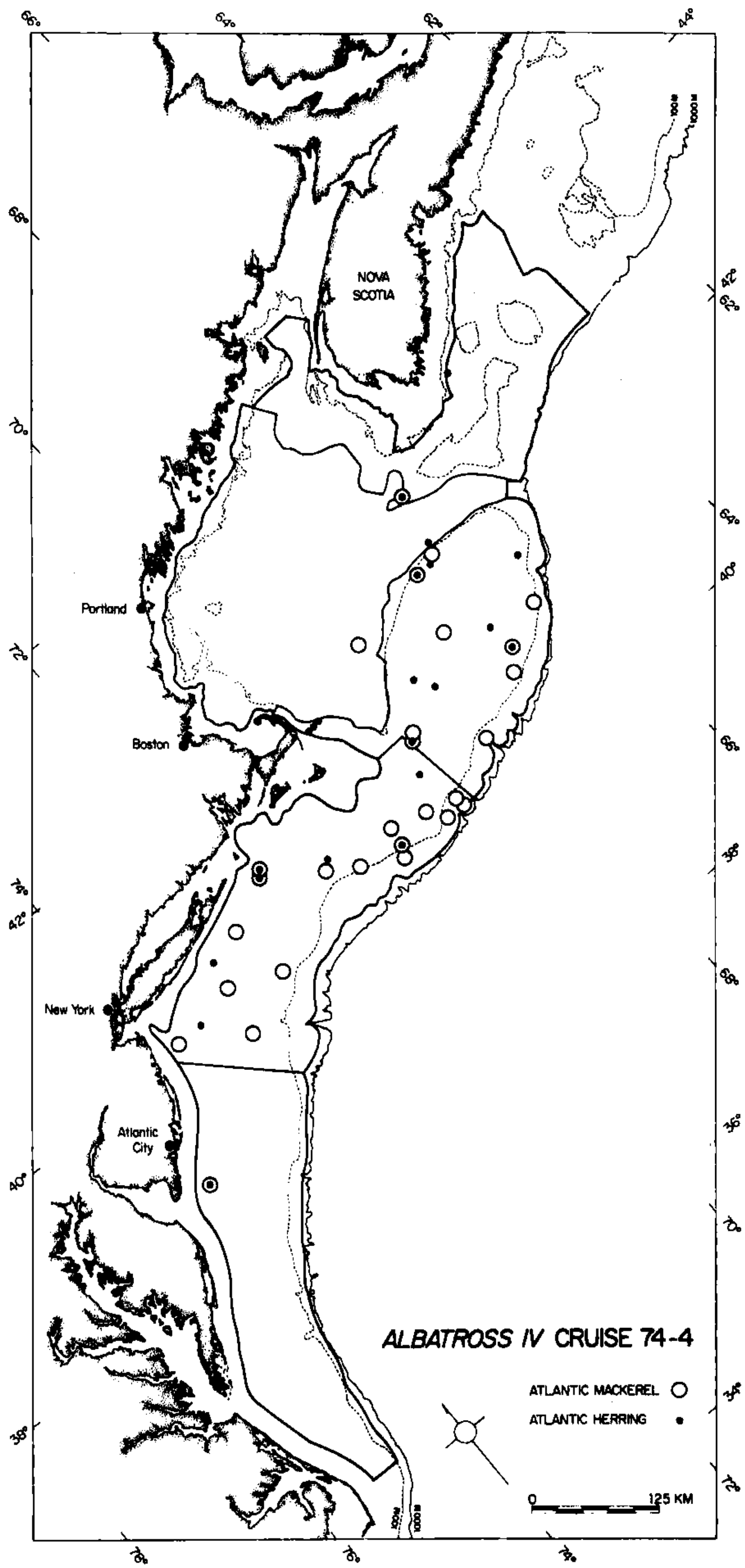

Fig. 1.

Chart showing the geographic distribution of stations at which herring and mackerel were sampled for this study.

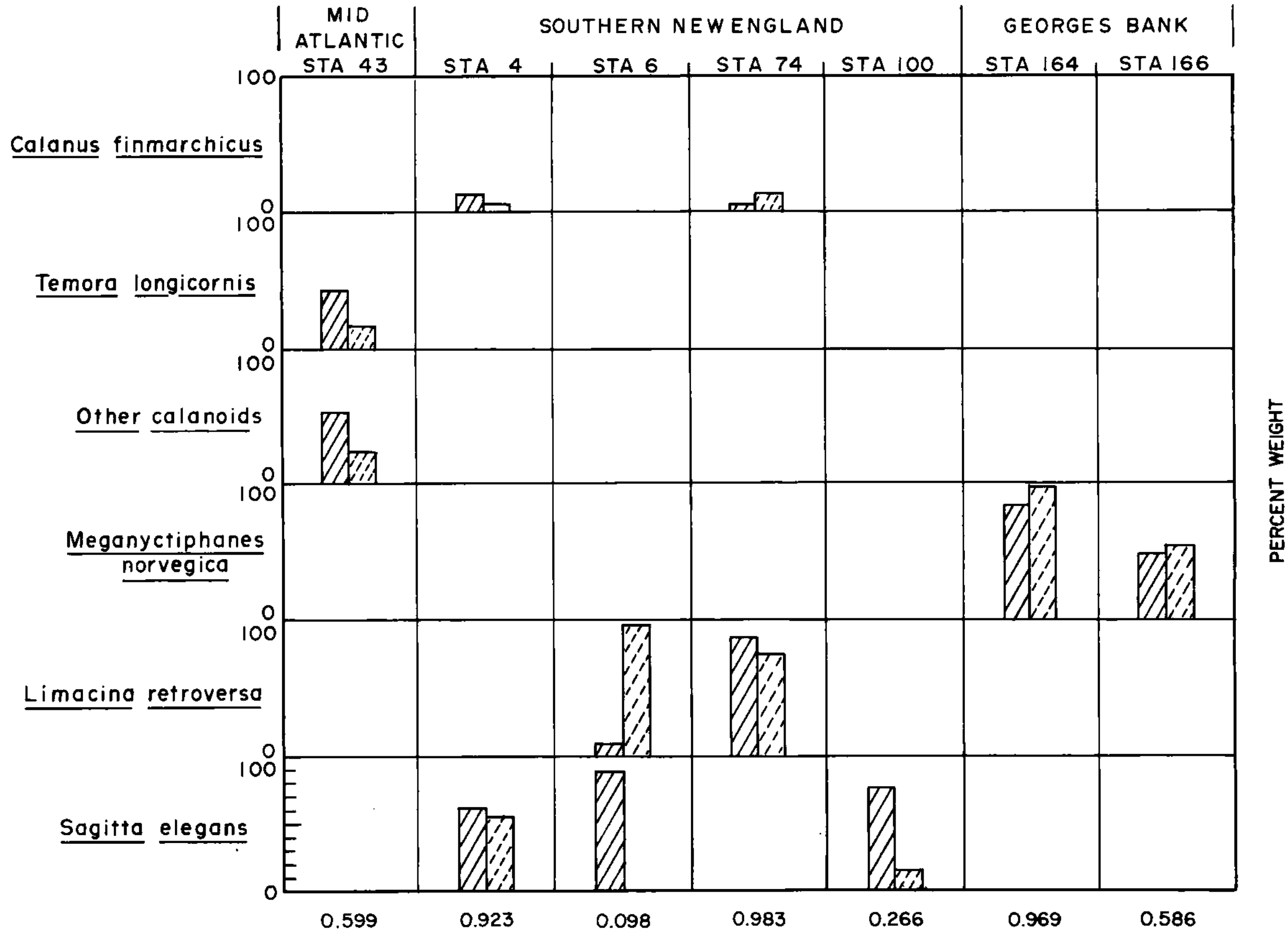

Fig. 2. The contribution of key prey species to the quantitative food habits of herring and mackerel sampled concurrently. The overlap index, C_{λ}, appears at the bottom of each station column.