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Food of Fifteen Northwest Atlantic Gadiform Fishes

Richard W. Langton and Ray E. Bowman

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U.S. DEPARTMENT OF COMMERCE
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721. National Marine Fisheries Service survey of trace elements in the fishery resource. By R. A. Hall, E. G. Zook, and G. M. Meaburn. March 1978, iii + 313 p., 5 tables, 3 app. figs., 1 app. table.

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Philip M. Klutznick, Secretary
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Richard A. Frank, Administrator
National Marine Fisheries Service
Terry L. Leitzell, Assistant Administrator for Fisheries

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Food of Fifteen Northwest Atlantic Gadiform Fishes

RICHARD W. LANGTON and RAY E. BOWMAN[1]

ABSTRACT

The food of 15 species of gadiform fishes occurring in the northwest Atlantic, from Cape Hatteras, N.C., to Nova Scotia, have been investigated for the years 1969-72. The popolations of Atlantic cod, *Gadus morhua*; pollock, *Pollachius virens*; silver hake, *Merluccias bilinearis*; white hake, *Urophycis tenuis*; offshore hake, *Merluccius albidus*; and cusk, *Brosme brosme*; have reasonably similar diets, being primarily piscivorous. The red hake, *Urophycis chuss*, and spotted hake, *Urophycis regius*, also have similar diets and are mixed feeders, preying on both fish and invertebrates. The final seven species, haddock, *Melanogrammus aeglefinus*; longfin hake, *Phycis chesteri*; fourbeard rockling, *Enchelyopus cimbrius*; marlin-spike, *Nezumia bairdi*; longnose grenadier, *Coelorhynchus carminatus*; fawn cusk-eel, *Lepophidium cervinum*; and ocean pout, *Macrozoarces americanus*; prey almost exclusively on invertebrates.

INTRODUCTION

Investigations on the food habits of fish have been a major topic of research since the beginning of fishery research as a scientific discipline. Since food availability ultimately controls production, the literature has become replete with papers describing, in detail, the prey of numerous species of fish. This vast literature has concentrated on the more common commercially important species, often at the expense of the lesser known but ecologically interesting fish. Among the Gadiformes described in this report the literature on the cod and haddock was found to be the most extensive (see Literature cited), reflecting the importance of the fishery for these two animals, while comparative data on the food habits of fish such as the spotted hake, red hake, and the grenadiers is either scanty or completely lacking, especially for fish from the northwest Atlantic.

In recent years some authors have suggested that management of a single fish species is untenable and that, instead, the ecosystem must be considered as a whole (Gulland 1977). The commercially important species must be considered in relation to their role in the total marine environment. Edwards (1976) has gone so far as to say that, in the context of total ecosystem management, fish could be ignored as individual species and considered as a group occupying a specified feeding niche. These niches are dependent upon the fishes' food habits which are, in turn, related to the morphology and size of the fish. Food related size classes for fish have been identified as "threshold lengths" by Parker and Larkin (1959) or "feeding stanzas" by Paloheimo and Dickie (1965) and Tyler (1972). In order to develop such a management plan, however, it is first necessary to describe quantitatively the food of all the major fish populations occurring within the bounds of the ecosystem and evaluate the role of each stock relative to the other fish in that same system.

This report describes the food of 15 northwest Atlantic gadiform fish populations.

METHODS

Fish utilized for stomach contents analysis were collected during six bottom trawl survey cruises conducted on the following dates: 8 October-23 November 1969; 3 September-20 November 1970; 9 March-1 May 1971; 30 September-19 November 1971; 8 March-24 April 1972; and 27 September-20 November 1972. Collections were made with a # 36 Yankee otter trawl with rollers, 9 m legs, and standard 544 kg oval doors. The cod end and upper belly were lined with 13 mm mesh netting to retain smaller fish. A scheme of stratified random sampling was conducted within the five geographic areas of the northwest Atlantic (Fig. 1) and sampling continued over 24 h per day.[2]

A total of 9,158 stomachs was collected from 15 species of the Gadiformes. The fish were selected randomly from the bottom trawl survey catch. Stomachs were excised aboard ship; labeled according to species, cruise, and station; and preserved in 10% Formalin. The general plan was to obtain a random sample of the population for each species, without bias toward a specified length or sex. Juvenile fish were preserved whole. Only fish above a specified length are considered in this paper. The species collected and their minimum fork lengths are as follows: Atlantic cod, *Gadus morhua* (Linneaus), >20 cm; haddock, *Melanogrammus aeglefinus* (Linnaeus), >20 cm; silver hake, *Merluccius bilinearis* (Mitchill), >20 cm; pollock, *Pollachius virens* (Linnaeus),

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[2]Further details of the bottom trawl techniques may be obtained from the Resource Surveys Investigation, Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

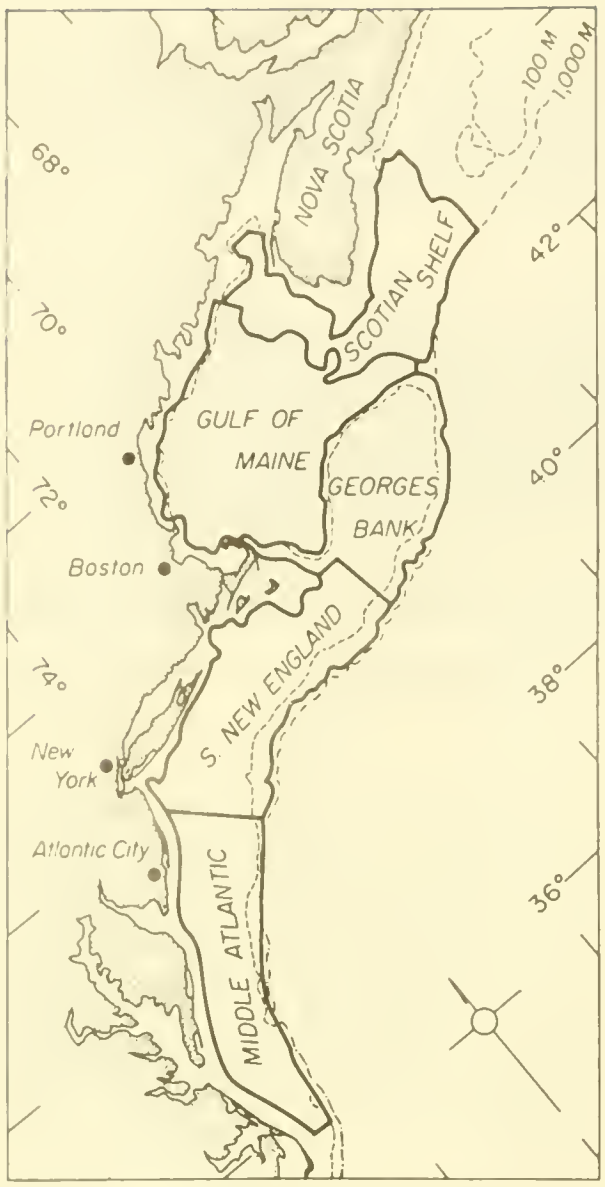

Figure 1.—Five geographic areas of the northwest Atlantic composing the sampling area for fish food studies, 1969-72.

>20 cm; red hake, *Urophycis chuss* (Walbaum), >20 cm; white hake, *Urophycis tenuis* (Mitchill), >20 cm; spotted hake, *Urophycis regius* (Walbaum), >10 cm; longfin hake, *Phycis chesteri* Goode and Bean, >10 cm; offshore hake, *Merluccius albidus* (Mitchill), >20 cm; fourbeard rockling, *Enchelyopus cimbrius* (Linnaeus), >10 cm; cusk, *Brosme brosme* (Müller), >20 cm; marlin-spike, *Nezumia bairdi* (Goode and Bean), >10 cm; longnose grenadier, *Coelorhynchus carminatus* (Goode), >10 cm; fawn cusk-eel, *Lepophidium cervinum* (Goode and Bean), >10 cm; and the ocean pout, *Macrozoarces americanus* (Bloch and Schneider), >10 cm.

In the laboratory, the preserved stomachs were opened and the contents emptied onto a fine mesh screen to permit washing without losing any food items. The various prey items were manually sorted, identified to the lowest possible taxa (using a dissecting microscope when necessary), and damp dried on bibulous paper. Each taxonomically distinct group was weighed to the nearest 0.01 g on a Mettler balance, immediately after blotting. Parasites in the stomach were included as part of the stomach contents and are incorporated in the tables under "Other Groups."

Food

The food of each species of fish is summarized on a weight basis as a percentage of the total weight of stomach contents. In the tables the subtotals for the major prey categories, i.e., subtotals for the major taxa, are offset and italicized. The tables follow a standard format to facilitate comparison of the food between species. In the text the broader groupings of prey, as presented in the tables, are discussed in detail. The percentage weight is included in parentheses after the first mention of a prey group in order to quantify that particular prey's significance in the diet at that taxonomic level.

Dietary Overlap

Percentage similarity, as a measure of dietary overlap, was calculated according to the formula of Shorygin (Ivlev 1961) as follows:

$$P.S. = 100 - 0.5\Sigma|a-b|$$

or, more simply, by summing the smaller value, in this case the percentage weight, for all prey shared by the two predators. Accordingly:

$$P.S. = \Sigma \min (a,b)$$

where: P.S. = percent similarity
a = percentage weight for a given prey group for predator A
b = percentage weight of the same prey group for predator B.

If a +, indicating <0.1% weight, was the smallest value for any prey group in the table it was arbitrarily assigned a value equal to 0.05% for the calculations.

RESULTS

Food

Since the data are presented as percentages it is possible to compare the food of each species directly and independently of the sample size. A detailed comparison of food between species will be made later but first we consider separately the food of each species over the entire study area (Table 1, Fig. 2) and then by the geographic areas (remaining tables) shown in Figure 1.

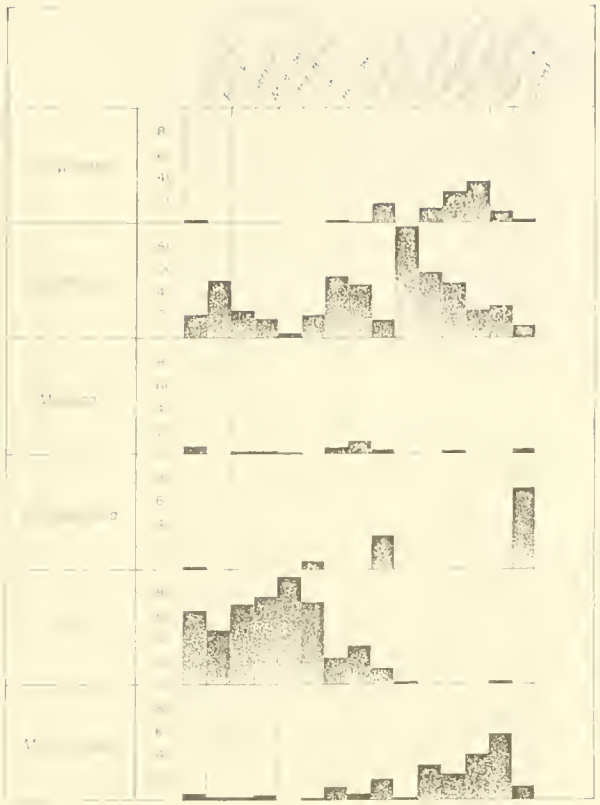

Figure 2.—Diagrammatic representation of prey of 15 gadiform fishes from five geographic areas in the northwest Atlantic for both spring and autumn bottom trawl survey cruises, 1969-72. Data are expressed as percentage weight.

Atlantic cod, *Gadus morhua*.—Atlantic cod preyed most heavily on fish (64.0%). Clupeidae (27.4%) were the most important prey, with the Atlantic herring, *Clupea harengus* (16.7%), being the largest single contributor to the diet. The Gadidae made up 3.7% of the diet while the Scombridae, represented exclusively by the Atlantic mackerel, *Scomber scombrus*, composed 3.1% of the diet. The Scorpaenidae contributed 3.2% to the diet, of which 2.6% was identified as the redfish, *Sebastes marinus*. After fish, the crustaceans were the next most important prey group, making up 20.7% of the diet by weight. Decapods were the most important crustaceans totaling 16.6% of the diet. The Cancridae, represented by both species of *Cancer*, i.e., *C. borealis* (1.5%) and *C. irroratus* (1.4%), constituted a major part of the decapod prey totaling 4.7% of the diet. Pandalid shrimp (2.9%), particularly *Dichelopandalis leptocerus* (1.3%), and the toad crabs (2.1%) (family Majidae) of the genus *Hyas* also accounted for part of the decapod prey. Other phyla played a less important role. Mollusca composed only 7.6% of the prey with the pelecypods *Placopecten* (2.9%) and *Pecten* (1.2%) contributing the major fraction. Scallops were important only on Georges Bank and may represent the remains of scallops discarded by fishermen which were then preyed upon by cod. A similar situation was observed for Georges Bank haddock by Wigley (1956). Polychaetes and echinoderms composed an even smaller percentage of the diet, 1.3 and 1.2%, respectively.

Pollock, *Pollachius virens*.—Almost one-half of the pollock's diet was fish (47.0%). The majority were clupeids (19.2%) which were identified as Atlantic herring (14.3%). Gadids (1.4%) were also preyed on, especially silver hake (1.2%), and in one instance a juvenile pollock was identified as part of the stomach contents. A small percentage of the stomach contents was made up of the scorpaenid *Sebastes marinus* (1.5%). "Other Pisces" (24.9%) accounted for over half the fish, and in this category eels (5.7%), lanternfish (2.0%), and the American sand lance, *Ammodytes americanus* (0.1%), could be identified. The remaining half of the diet consisted exclusively of crustaceans (50.8%). Euphausiids (35.3%) made up the majority of the Crustacea, with *Meganyctiphanes norvegica* contributing 26.5% of the diet by weight. Other species of euphausiids, such as *Thysanoessa inermis*, *T. longicaudata*, and *Euphausia krohnii*, were also identified in the stomach contents, but each of these species contributed <1% to the total weight of the prey consumed. Pandalid shrimp (2.5%) of the genera *Pandalus* (1.8%) and *Dichelopandalus* (0.5%) were of secondary importance, while *Pasiphaea multidentata* (10.0%), a pelagic shrimp, listed under "Other Decapoda," was of major significance. Annelids (polychaetes), molluscs, echinoderms, and other phyla contributed only 1% of the total diet.

Silver hake, *Merluccius bilinearis*.—The major proportion of the silver hake's diet was fish (70.9%). These hake preyed heavily on Atlantic mackerel (18.9%) and on clupeids (14.6%) such as the Atlantic herring (10.4%) and the alewife, *Alosa pseudoharengus* (4.2%). Silver hake were also cannibalistic; 3.4% of the Gadidae (7.1%) were silver hake. A large part of the fish could not be identified due to their state of digestion. Consequently, 30.1% of the prey was included under "Other Pisces." However, two groups in this category that could be recognized were the butterfish, *Peprilus triacanthus* (1.5%), and the lanternfish (family Myctophidae) (1.1%). Crustaceans formed the remaining bulk of the diet, 25.0%. Euphausiids (12.6%), such as *Meganyctiphanes norvegica* (7.4%), were the single most important crustaceans, but the pandalid shrimp, *Dichelopandalus leptocerus* (3.2%), was also of some importance. Other crustaceans which contributed to the diet were the two caridean shrimp: *Crangon septemspinosa* (1.4%) and *Pasiphaea* (2.0%). The only molluscs of any note were the cephalopods (2.2%), such as the squid *Loligo* (1.5%).

White hake, *Urophycis tenuis*.—White hake preyed heavily on fish (78.2%). The clupeids (12.5%) were the single most important group, with Atlantic herring making up 4.8% of the total diet. Gadids (10.7%) were also important, with silver hake (3.0%), red hake (0.8%), Atlantic cod (0.5%), haddock (0.5%), longfin hake (0.3%), and white hake (0.2%) all having been identified

Table 1.—Stomach contents of 15 northwest Atlantic gadiform fishes, expressed as percentage weight,

Prey/Predators	Atlantic cod	Pollock	Silver hake	White hake	Offshore hake	Cusk	Red hake
POLYCHAETA	*1.3*	*0.1*	*0.2*	*0.2*	–	–	*2.9*
Nereidiformia	1.2	+	0.2	0.1	–	–	1.3
Terebelliformia	+	–	–	–	–	–	+
Sabelliformia	–	–	–	–	–	–	0.1
Other Polychaeta	0.1	+	+	0.1	–	–	1.5
CRUSTACEA	*20.7*	*50.8*	*25.0*	*17.3*	*5.5*	*20.4*	*54.1*
Amphipoda	0.5	0.1	0.4	0.1	–	+	7.4
Mysidacea	0.1	+	0.2	+	–	–	0.1
Euphausiacea	2.1	35.3	12.6	4.3	1.1	0.3	3.0
Pandalidae	2.9	2.5	5.3	9.1	2.5	4.1	12.1
Crangonidae	0.3	+	1.4	0.3	–	–	3.0
Axiidae	0.5	–	+	0.1	–	–	2.0
Paguridae	1.7	–	–	+	–	–	2.8
Majidae	2.1	–	–	–	–	1.7	0.1
Cancridae	4.7	–	0.1	0.3	–	–	5.3
Other Decapoda	4.4	10.4	2.6	2.3	1.9	11.6	13.4
Other Crustacea	1.4	2.4	2.4	0.8	–	2.7	4.9
MOLLUSCA	*7.6*	*0.4*	*2.2*	*2.1*	*0.9*	–	*6.3*
Gastropoda	2.4	0.4	+	+	–	–	3.1
Pelecypoda	4.3	+	+	+	–	–	+
Cephalopoda	0.1	+	2.2	2.1	0.9	–	1.3
Other Mollusca	0.8	+	+	+	–	–	1.9
ECHINODERMATA	*1.2*	–	+	+	–	*6.8*	*0.6*
Echinoidea	0.1	–	–	–	–	–	0.1
Ophiuroidea	0.6	–	+	+	–	6.8	–
Other Echinodermata	0.5	–	+	–	–	–	0.5
PISCES	*64.0*	*47.0*	*70.9*	*78.2*	*93.4*	*71.5*	*25.3*
Clupeidae	27.4	19.2	14.6	12.5	–	–	0.5
Gadidae	3.7	1.4	7.1	10.7	59.9	–	0.4
Scombridae	3.1	–	18.9	7.3	–	–	0.4
Scorpaenidae	3.2	1.5	–	1.7	–	–	–
Bothidae	0.3	–	–	–	–	–	0.5
Pleuronectidae	2.5	–	0.1	–	–	–	0.1
Other Pisces	23.8	24.9	30.1	46.0	33.5	71.5	23.5
Other groups	*0.4*	*0.5*	*0.1*	*0.1*	+	*0.2*	*0.8*
Animal remains	*3.2*	*1.2*	*1.6*	*2.1*	*0.2*	*0.9*	*9.6*
Sand and rock	*1.6*	*0.1*	+	+	–	*0.2*	*0.3*
Number of stomachs	1,541	639	2,152	912	73	72	1,110
Percentage of empty stomachs	7.6	11.8	32.8	23.9	57.5	73.6	15.9
Mean weight per stomach (g)	27.9	18.2	2.5	18.0	2.4	3.2	2.3
Mean predator fork length (cm)	54.7	46.8	27.5	46.4	32.2	63.0	30.3
Number of sampling stations	291	160	222	177	14	43	154

in the stomach contents. The Atlantic mackerel (7.3%) was also important prey. Manfyy of the fish in the category "Other Pisces" (46%) were identified. Among those fish that could be identified to species were the argentine, *Argentina silus* (8.9%); wrymouth, *Cryptocanthodes maculatus* (0.8%); American sand lance (0.7%); and the butterfish (0.4%). Crustacea (17.3%) constituted most of the remainder of the diet. Of primary importance in this group were the pandalid shrimp (9.1%) of which four species have been identified, *Pandalus borealis* (2.2%), *Dichelopandalus leptocerus* (0.8%), *P. montagui* (0.5%), and *P. propinquus* (<0.1%). Euphausiids (4.3%), such as *Meganyctiphanes* (2.1%) and *Thysanoessa inermis* (0.3%), were also of some dietary significance. Rock crabs of the family Cancridae, i.e., *C. borealis* (0.2%) and *C. irroratus* (0.1%), were also identified as prey. Similarly, *Crangon* (0.2%) was identified as being of minor dietary importance. Among the "Other Decapoda," the red crab, *Geryon* (0.9%), was the most important. The only other category that contributed to the diet to any degree was cephalopods (2.1%) of the genera *Loligo* (1.2%) and *Rossia* (0.1%).

Offshore hake, *Merluccius albidus*.—Offshore hake preyed most heavily on fish, which accounted for 93.4% of the diet. The Gadidae contributed 59.9% of the diet by weight but none of the remains in the stomachs could be identified to lower than the family level. None of the fish remains in the "Other Pisces" category (33.5%) could be identified. Crustaceans were of secondary importance (5.5%) and those that could be identified were the two genera of pandalid shrimp (2.5%), *Dichelopandalus leptocerus* (2.4%) and *Pandalus* (0.1%). Euphausiids (1.1%), in particular *Meganyctiphanes norvegica* (0.9%), were of little dietary significance. The only other decapod identified was the pelagic shrimp *Pasiphaea* (0.9%).

Cusk, *Brosme brosme*.—Cusk are primarily fish eaters (71.5%) but none of the prey species could be identified from the digested remains found in the stom-

collected during the spring and autumn bottom trawl survey cruises, 1969-72. (+ indicates present but <0.1%.)

Spotted hake	Haddock	Longfin hake	Fourbeard rockling	Marlin-spike	Longnose grenadier	Fawn cusk-eel	Ocean pout
0.5	*17.6*	–	*12.5*	*27.5*	*35.8*	*9.9*	*3.3*
0.1	2.0	–	–	–	–	2.4	3.0
–	1.6	–	–	–	–	–	+
–	1.3	–	–	–	–	–	–
0.4	12.7	–	12.5	27.5	35.8	7.5	0.3
47.5	*16.2*	*97.6*	*57.4*	*47.3*	*24.8*	*28.8*	*11.1*
7.3	6.4	+	1.0	7.8	–	4.9	5.6
+	0.1	–	+	4.0	–	–	–
+	2.6	60.3	1.0	+	–	–	–
3.9	1.4	8.7	9.6	–	–	–	+
4.1	0.1	–	40.7	–	–	6.4	+
+	0.9	–	–	–	–	0.3	–
0.1	0.4	–	–	–	–	+	0.5
+	0.3	–	–	–	–	–	0.3
6.8	0.1	–	–	–	–	–	2.9
20.8	1.8	15.4	4.7	27.5	23.6	0.7	0.8
4.5	2.1	13.2	0.4	8.0	1.2	16.5	1.0
11.5	*3.1*	–	–	*2.5*	–	*0.2*	*4.0*
0.1	0.3	–	–	–	–	–	0.6
0.2	2.3	–	–	2.5	–	–	3.3
11.2	0.2	–	–	–	–	–	–
+	0.3	–	–	–	–	0.2	0.1
+	*29.9*	*0.3*	–	–	–	*0.5*	*70.7*
–	5.7	0.3	–	–	–	–	64.9
–	21.6	–	–	–	–	0.2	5.3
+	2.6	–	–	–	–	0.3	0.5
34.2	*14.6*	*1.1*	+	–	+	*2.3*	*0.1*
–	12.9	–	–	–	–	–	–
4.3	0.3	–	–	–	–	–	–
3.3	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–
1.8	–	–	–	–	–	–	–
0.8	+	–	–	–	–	–	–
24.0	1.4	1.1	+	–	+	2.3	0.1
+	*1.0*	+	+	–	*2.8*	*29.8*	*2.7*
5.9	*8.9*	*1.0*	*30.1*	*22.4*	*36.6*	*28.5*	*4.0*
0.3	*8.7*	–	–	*0.3*	–	+	*4.1*
876	1,131	126	48	23	11	109	377
14.3	7.3	62.7	12.5	8.7	36.4	22.9	25.9
1.1	6.8	0.28	0.30	0.14	0.09	0.03	6.9
18.4	45.6	23.6	24.2	24.2	19.3	22.3	46.0
64	154	15	10	4	4	13	65

achs. Crustaceans are also a major prey category, 20.4%. Within this group the toad crab (Majidae), *Hyas coarctatus* (1.7%), and several species of pandalid shrimp (4.1%), *Pandalus borealis* (3.3%), *P. propinquus* (0.1%), and *Dichelopandalus leptocerus* (0.7%), were identified. The Penaeidea (1.3%) also contributed a small amount to the diet. The brittle star, *Ophiopholus aculeata* (6.8%), was the only echinoderm preyed upon.

Red hake, *Urophycis chuss*.—Crustaceans (54.1%) were the major prey of red hake. A number of different families contributed to the diet, with the Pandalidae (12.1%), especially the genus *Dichelopandalus* (7.1%), being of primary importance. The galatheid crab, *Munida* (10.2%), which is included under "Other Decapoda," was also a major dietary component. Of secondary importance were the Cancridae (5.3%), particularly *C. irroratus* (2.1%); the Crangonidae (3.0%); the Axiidae (2.0%); *Axius* (0.6%); *Calocaris* (1.2%); and a variety of different species of amphipods (7.4%). Fish were also important prey (25.3%). Clupeids (0.5%), Atlantic mackerel (0.4%), and the gadids (0.4%), such as silver hake (0.2%) and other red hake (0.2%), all contributed to the diet. The flatfish prey included Gulf Stream flounder, *Citharichthys arctifrons* (0.5%), and the winter flounder, *Pseudopleuronectes americanus* (0.1%). Among the category "Other Pisces" (23.5%), the wrymouth (1.1%) and the snake eel, *Omochelys cruentifer* (0.9%), were identified. The Mollusca also contributed to the diet (6.3%), however, most of them were not identifiable to below the class level. Of the gastropods consumed, only *Buccinum* (0.2%) was identified to the genus level. Polychaetes were also a minor prey group (2.9%), and a few genera that could be identified from the partially digested remains were *Arenicola* (0.1%), *Nephtys* (0.3%), *Sabella* (0.1%), *Aphrodita* (0.1%), and *Ophioglycera* (0.1%).

Spotted hake, *Urophycis regius*.—Crustacea (47.5%) form almost half the diet of spotted hake. Among the most important contributors to this assemblage of crustaceans were the galatheid crabs, *Munida iris*

(8.8%), *M. valida* (4.5%), remains of *Munida* (3.1%) that could not be identified to species, and other galatheids of the genus *Munidopsis* (1.7%). These crabs form the majority of the animals in the category "Other Decapoda" and were the single most important prey. Other crustaceans of some significance were amphipods (7.3%), especially the Hyperiidae (4.4%); the rock crab, *Cancer irroratus* (4.2%); the Crangonidae (4.1%), such as *Crangon* (3.9%) and *Pontophilus* (0.1%); the pandalid shrimp, *Dichelopandalus* (3.7%); and lastly, isopods (2.0%), which are included in the category "Other Crustacea." Fish constituted over one-third of the spotted hake's diet, 34.2%. Gadids (4.3%), such as silver hake (2.2%) and red hake (2.1%), were important prey, along with the Atlantic mackerel (3.3%). The bothid prey included the Gulf Stream flounder (1.8%), whereas the only member of the Pleuronectidae identified was the yellowtail flounder, *Limanda ferruginea* (0.5%). Fish, considered under the category "Other Pisces," that could be identified were cusk-eel (family Ophidiidae) (4.4%), lanternfish (family Myctophidae) (3.0%), primarily of the genus *Myctophum* (1.5%), and the snake eel (0.1%). The only other taxon that was of significance as prey is the Mollusca (11.5%). Within this phylum, Cephalopoda (11.2%) was the most important class. Two genera of squid were identified in the stomachs: *Loligo* (4.2%) and *Rossia* (0.4%). Most of the remaining cephalopods (6.6%) could not be identified.

Haddock, *Melanogrammus aeglefinus*.—Haddock fed on a variety of benthic invertebrates with echinoderms (29.9%) of the subclass Ophiuroidea (21.6%) being of major importance. The brittle stars *Ophiura* (6.2%) and *Ophiopholis* (5.5%) were the two most important prey items. Polychaetes, crustaceans, and fish all contributed about equally to the diet, 17.6%, 16.2%, and 14.6%, respectively. A number of different polychaetes were identified in the stomach contents, e.g., *Aphrodita* (0.5%), *Cistenidae* (0.2%), *Chone infundibulinformis* (0.1%), Sabella (0.1%), and *Nephtys* (0.1%). The single most important species was *Ammotrypane aulogaster* (3.8%) which accounted for more than one-fourth of the category "Other Polychaeta" (12.7%). Amphipods (6.4%), particularly gammaridean amphipods (4.2%), were the largest component of the crustacean prey. Other crustaceans of importance were euphausiids (2.6%), such as *Meganyctiphanes norvegica* (1.8%), and the pandalid shrimp (1.4%), *Pandalus* (0.7%) and *Dichelopandalus leptocerus* (0.5%). The importance of fish may be slightly overemphasized from the present results. The Clupeidae appear to be a major food source; however, the entire weight (12.9%) was due to the consumption of herring eggs rather than adult or juvenile fish. Finally, sand and rocks made up 8.7% of the stomach contents by weight, thus reflecting the haddock's benthic habits.

Longfin hake, *Phycis chesteri*.—The longfin hake preyed primarily on Crustacea, as this prey group made up 97.6% of the diet. However, the total quantity of prey examined was relatively small (35.28 g) although it represented 126 fish. Possibly a more extensive study of the food of this fish would broaden the spectrum of prey consumed. Nevertheless, in this study the single most important prey item was the euphausiid, *Meganyctiphanes norvegica*, which constituted more than half (55.9%) of the diet. The only other crustacean identified to the genus level was the shrimp, *Pandalus* (8.6%).

Fourbeard rockling, *Enchelyopus cimbrius*.—A large proportion of the diet of the fourbeard rockling was Crustacea (57.4%). The primary prey species was *Crangon septemspinosa* (40.7%). The pandalid shrimp, *Dichelopandalus leptocerus* (9.6%), was of secondary importance, while euphausiids (1.0%) and amphipods (1.0%) contributed little to the diet. Polychaetes (12.5%) were also preyed upon but the only identifiable genus was *Ammotrypane* (3.3%). Unidentified animal remains made up 30.1% of the diet. This is due to the state of digestion of the prey and also, possibly, because of the small total weight in the stomachs (14.4 g).

Marlin-spike, *Nezumia bairdi*.—This summary of the food of the marlin-spike is based on only 23 fish and an extremely small weight (3.22 g) for the prey. The two most important prey groups were the crustaceans (47.3%) and polychaetes (27.5%). The polychaete remains could not be identified below the class level. Some of the crustaceans were identifiable, such as hippolytid shrimp, *Eualus pusiolus* (26.0%), which accounts for most of the animals included in "Other Decapoda." Mysids, *Neomysis americana* (4.0%), the isopod, *Cirolina* (0.6%), and euphausiids (<0.1%) were the other crustaceans that could be identified.

Longnose grenadier, *Coelorhynchus carminatus*.—As has been described for the marlin-spike, the summary of the food of longnose grenadier is based on a small sample both in the number of fish analyzed and the total weight of prey. It is possible that the percentage composition of the diet would differ markedly if more fish were available for analysis. From the available data, polychaetes and decapod shrimp were the only identifiable prey.

Fawn cusk-eel, *Lepophidium cervinum*.—The stomach contents of 109 fawn cusk-eel were examined, but the total weight of the prey amounted to only 3.27 g. For this reason the percentage weights listed in Table 1 should be used more as a qualitative guide to the food since a small change in weight could markedly influence the percentage composition of the diet. Bearing this precaution in mind, the prey items are discussed below.

The most significant prey group was the crustaceans (28.8%). Within this group the "Other Crustacea" were the largest contributors, primarily the isopod, *Cirolina* (12.6%). A variety of different families of amphipods was found in the stomachs, the most important being the Gammaridae (4.6%). Other crustaceans that could be identified were two members of the *Crangonidae* (6.4%), [*Crangon* (2.3%) and *Sabinea* (2.6%)], the munid crab,

Munidopsis (0.7%), and the mud shrimp, *Calocaris* (0.3%). Polychaetes (9.9%) were moderately important, with a few identified to the genus level, such as *Nephtys* (1.8%), *Scalibregma* (1.0%), and *Nothria* (0.6%). "Other Groups" (29.8%) was the single most important category contributing to the stomach contents, and this was comprised of a large number of parasitic nematodes (29.4%).

Ocean pout, *Macrozoarces americanus*.—Ocean pout preyed most heavily on echinoderms (70.7%), the single most important species being the sand dollar, *Echinarachnius parma* (56.3%). Ophiuroids (5.3%), such as *Ophiopholis* (1.1%) and *Ophiura* (0.1%), were also identified in the stomach contents. Crustaceans (11.1%), most notably the rock crabs of the family Cancridae (2.9%), both *Cancer irroratus* (1.0%) and *C. borealis* (0.7%), and a number of different amphipods (5.6%) were also prey items. Polychaetes (3.3%) of the genus *Aphrodita* (3.0%) and the tunicate, *Cnemidocarpa mollis* (1.7%), which falls into the category "Other Groups," were other components of the diet.

Geographic Comparisons

The data on the food of the 15 species of Gadiformes for each of the five geographic areas (Fig. 1) in the northwest Atlantic are presented in the following text and/or Tables 2-11. In this section the data are compared and contrasted for each species in each of the five areas to emphasize similarities and differences in food over these broad geographic regions.

Atlantic cod, *Gadus morhua*.—In all of the geographic areas fish was the major prey of Atlantic cod with the Clupeidae generally being the most important (Table

Table 2.—Geographic breakdown of food of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. Data are expressed as percentage weight, for fish collected during the spring and autumn bottom trawl survey cruises 1969-72. (+ indicates present but <0.1%.)

Prey	Middle Atlantic	Southern New England	Georges Bank	Gulf of Maine	Western Nova Scotia
POLYCHAETA	*0.1*	*6.4*	*1.1*	*0.3*	*0.8*
Nereidiformia	0.1	6.4	1.0	0.2	0.6
Terebelliformia	–	–	+	+	+
Sabelliformia	–	–	–	–	–
Other Polychaeta	–	+	0.1	0.1	0.2
CRUSTACEA	*10.2*	*20.9*	*15.2*	*26.1*	*27.6*
Amphipoda	+	1.6	0.7	0.1	0.1
Mysidacea	–	+	0.2	+	+
Euphausiacea	–	–	0.4	1.2	8.8
Pandalidae	0.1	0.7	3.1	2.8	3.9
Crangonidae	1.4	0.3	0.4	0.1	0.1
Axiidae	–	2.4	0.1	+	1.3
Paguridae	3.8	0.9	2.5	0.2	2.2
Majidae	–	+	1.5	0.2	7.4
Cancridae	2.8	12.8	4.4	5.9	–
Other Decapoda	–	1.6	0.7	14.1	1.7
Other Crustacea	2.1	0.6	1.2	1.5	2.1
MOLLUSCA	*0.6*	*1.9*	*15.6*	*0.7*	*0.6*
Gastropoda	–	1.4	4.7	0.3	0.3
Pelecypoda	–	0.4	9.4	0.1	+
Cephalopoda	–	+	+	0.3	+
Other Mollusca	0.6	0.1	1.5	+	0.3
ECHINODERMATA	–	*0.8*	*0.6*	*0.4*	*3.6*
Echinoidea	–	+	+	+	0.2
Ophiuroidea	–	0.3	0.3	0.2	1.9
Other Echinodermata	–	0.5	0.3	0.2	1.5
PISCES	*86.5*	*64.1*	*61.6*	*69.5*	*60.6*
Clupeidae	–	32.8	37.3	23.3	12.1
Gadidae	12.9	–	2.6	4.5	6.5
Scombridae	–	6.4	–	8.7	1.7
Scorpaenidae	–	–	–	11.6	0.9
Bothidae	–	1.9	0.3	–	–
Pleuronectidae	43.7	–	4.3	–	–
Other Pisces	29.9	23.0	17.1	21.4	39.4
Other groups	+	*0.1*	*0.6*	*0.3*	*0.3*
Animal remains	*2.6*	*4.8*	*2.7*	*2.2*	*5.4*
Sand and rock	+	*1.0*	*2.6*	*0.5*	*1.1*
Number of stomachs	7	79	667	347	441
Percentage of empty stomachs	0.0	6.3	6.9	8.6	8.1
Mean weight per stomach (g)	69.7	46.6	29.6	31.9	18.2
Mean predator fork length (cm)	82.0	65.8	50.3	57.7	57.9
Number of sampling stations	5	22	90	71	103

2). In the Middle Atlantic, however, only seven Atlantic cod stomachs were examined and yellowtail flounder (33.7%) was the most important prey. In Southern New England and on Georges Bank most of the clupeids could be identified as Atlantic herring (27.1 and 31.4%, respectively). The only other clupeid identified to species level was an alewife (0.9%), from Georges Bank.

A variety of other fish was eaten throughout the Northwest Atlantic and is listed by area as follows: Middle Atlantic—red hake (12.9%); winter flounder (10.0%); beardfishes, Polymyxiidae (9.0%); cusk-eels, Ophidiidae (6.4%); sand lance, *Ammodytes* (2.7%); and the longhorn sculpin, *Myoxocephalus octodecemspinosus* (1.5%). Southern New England—Atlantic mackerel (6.4%); windowpane, *Scophthalmus aquosus* (1.9%); Cryptacanthodidae (2.8%); the Cottidae (1.1%); and a seahorse, *Hippocampus* (0.2%). Georges Bank—yellowtail flounder (3.4%); American plaice, *Hippoglossoides platessoides* (0.9%); summer flounder, *Paralichthys dentatus* (0.1%); windowpane (0.2%); the rock gunnel, *Pholis gunnellus* (0.1%); sculpins such as the grubby, *Myoxocephalus aenaeus* (<0.1%), the longhorn sculpin (0.5%), and the mailed sculpin, *Triglops nybelini* (0.1%). Gulf of Maine—the scorpaenids, *Helicolenus dactylopterus* (1.9%) and *Sebastes marinus* (9.6%); Atlantic mackerel (8.7%); wolffish, *Anarhichadidae* (3.3%); *Argentina* sp. (3.2%); silver hake (1.6%); and the wrymouth (0.4%). Western Nova Scotia—sand lance (11.3%); gadids, including silver hake (1.7%), haddock (0.7%), and Atlantic cod (0.1%); Atlantic mackerel (1.7%); redfish (0.9%); wolffish (0.2%); and the rock gunnel (0.1%).

Crustacea were generally the second most important group of prey and, like fish, a variety of different crustaceans were consumed, but only the major groups will be discussed here. In the Middle Atlantic the only crustacean prey of any significance was hermit crabs, Paguridae (3.8%), and rock crabs (2.5%). Crustaceans composed 20.9% of the Atlantic cod's diet in Southern New England; and the rock crabs (12.8%), *Cancer borealis* (2.8%) and *C. irroratus* (1.8%), accounted for more than half of this group. On Georges Bank, rock crabs (4.4%) were again the most important crustacean prey but pandalid shrimp (3.1%) [i.e., *Dichelopandalus* (2.3%)], and hermit crabs, *Pagurus* (2.5%), also contributed to the diet. In the Gulf of Maine rock crabs (5.9%) and pandalid shrimp (2.8%) were again preyed upon but the red crab, *Geryon* (10.1%), was the most important decapod prey. Spider crabs (family Majidae) of the genus *Hyas* (7.4%) and euphausiids (8.8%), such as *Meganyctiphanes* (2.6%), were the primary crustacean prey in Western Nova Scotia. Of secondary importance were the Paguridae (2.2%) and the pandalid shrimp (3.9%), *Dichelopandalus leptocerus* (0.8%) and *Pandalus montagui* (0.3%).

Two other taxa were of some significance in two of the geographic areas. In Southern New England polychaetes of the suborder Nereidiformia made up 6.4% of the diet, and this was entirely due to the sea mouse, *Aphrodita*. The Mollusca accounted for 15.6% of the prey on Georges Bank. The pelecypods contributed most of the weight (9.4%), with the scallops, *Placopecten* (6.3%) and *Pecten* (2.6%), accounting for the majority of the prey in this group but these scallops may be scallop remains discarded by fishermen since only scallop viscera and no adductor muscles were found in the stomachs.

Pollock, *Pollachius virens*.—Because only six fish were collected for stomach content analysis in Southern New England and the Middle Atlantic, the following discussion is limited to the other three areas (Table 3).

The major prey of pollock on Georges Bank and in Western Nova Scotia was crustaceans (71.6 and 61.2%, respectively). In both of these areas euphausiids comprised more than one-half the diet. Of the euphausiids identified, *Meganyctiphanes norvegica* was the most important, contributing 46.6% of the diet on Georges Bank and 46.2% in Western Nova Scotia. Other euphausiids, such as *Thysanoessa longicaudata*, were preyed upon in both areas (3.6% on Georges Bank and <0.1% in Western Nova Scotia), but *Euphausia krohnii* (0.1%) was only found in stomachs collected from Georges Bank. Apart from euphausiids, pandalid shrimp, primarily *Pandalus* sp. (2.7% on Georges Bank and 2.9% in Western Nova Scotia), and "Other Decapoda" such as *Pasiphaea* (4.0% in Western Nova Scotia) were the only other important Crustacea. Fish accounted for the remaining bulk of the diet and a number of different species were identified in the stomach contents as follows: Georges Bank—lanternfish (8.8%); the pearlside, *Maurolicus pennanti* (1.2%); silver hake (0.4%); and pollock (0.1%). Western Nova Scotia—the snake eel (5.5%); redfish (1.3%); haddock (0.7%); silver hake (0.6%); blueback herring, *Alosa aestivalis* (0.5%); and the sand lance, *Ammodytes* (0.4%).

In the Gulf of Maine the emphasis shifted from Crustacea (33.8%) to Pisces (64.9%) as the major prey category. This difference was almost entirely caused by heavy predation on the Atlantic herring (29.4%). Few other fish, except for redfish (2.3%) and silver hake (1.9%), could be identified from the partially digested remains. Crustaceans remained an important prey group but the groups composing the category differed from those of Georges Bank and Western Nova Scotia. "Other Decapoda" were the most important, with *Pasiphaea* being the largest single prey item (5.5%). Euphausiids also contributed to the diet and, again, *Meganyctiphanes* (6.7%) was the most important, although *Thysanoessa inermis* (0.1%) was also present in the stomach contents. Finally, three species of pandalid shrimp were identified: *Dichelopandalus leptocerus* (0.9%), *Pandalus borealis* (0.6%), and *P. montagui* (<0.1%).

Silver hake, *Merluccius bilinearis*.—Silver hake are widespread with the result that stomachs were collected in reasonably large numbers from all geographic areas (Table 4). In all five areas fish was the major prey but the

Table 3.—Geographic breakdown of food of pollock, *Pollachius virens*, in the northwest Atlantic. Data are expressed as percentage weight, for fish collected during the spring and autumn bottom trawl survey cruises 1969-72. (+ indicates present but <0.1%.)

Prey	Middle Atlantic	Southern New England	Georges Bank	Gulf of Maine	Western Nova Scotia
POLYCHAETA	–	–	*0.1*	+	*0.1*
Nereidiformia	–	–	–	+	+
Terebelliformia	–	–	–	–	–
Sabelliformia	–	–	–	–	–
Other Polychaeta	–	–	0.1	+	0.1
CRUSTACEA	*92.7*	–	*71.6*	*33.8*	*61.2*
Amphipoda	–	–	0.5	+	+
Mysidacea	–	–	0.1	+	–
Euphausiacea	–	–	66.4	11.4	53.7
Pandalidae	–	–	2.9	2.1	3.1
Crangonidae	–	–	0.1	–	+
Axiidae	–	–	–	–	–
Paguridae	–	–	–	–	–
Majidae	–	–	–	–	–
Cancridae	–	–	–	–	–
Other Decapoda	–	–	0.4	16.0	4.2
Other Crustacea	92.7	–	1.2	4.3	0.2
MOLLUSCA	–	–	*1.6*	*0.1*	+
Gastropoda	–	–	1.6	–	–
Pelecypoda	–	–	–	–	+
Cephalopoda	–	–	–	0.1	+
Other Mollusca	–	–	–	–	–
ECHINODERMATA	–	–	–	–	–
Echinoidea	–	–	–	–	–
Ophiuroidea	–	–	–	–	–
Other Echinodermata	–	–	–	–	–
PISCES	*7.3*	*100.0*	*22.8*	*64.9*	*37.1*
Clupeidae	7.0	–	0.8	36.9	4.0
Gadidae	–	–	0.5	1.9	1.3
Scombridae	–	–	–	–	–
Scorpaenidae	–	–	–	2.3	1.3
Bothidae	–	–	–	–	–
Pleuronectidae	–	–	–	–	–
Other Pisces	0.3	100.0	21.5	23.8	30.5
Other groups	–	–	*1.3*	*0.3*	*0.3*
Animal remains	–	–	*2.6*	*0.8*	*1.3*
Sand and rock	–	–	+	*0.1*	+
Number of stomachs	5	1	206	203	224
Percentage of empty stomachs	20.0	0.0	2.9	12.8	18.8
Mean weight per stomach (g)	36.3	13.1	12.7	27.7	14.2
Mean predator fork length (cm)	51.0	82.0	38.2	66.4	44.6
Number of sampling stations	3	28	32	68	29

species of fish eaten differed. Gadids (13.5%) were of primary importance in the Middle Atlantic where silver hake were heavily cannibalistic (12.6%). Yellowtail flounder (0.7%) was the only pleuronectid eaten and some of the fish in the "Other Pisces" category were the butterfish (0.9%); horned lanternfish, *Ceratoscopelus maderensis* (0.6%); and the longhorn sculpin (0.1%). In Southern New England the Gadidae (12.6%) were also important and silver hake were again cannibalistic (7.4%). The Atlantic mackerel (31.7%), however, was the primary prey. "Other Pisces" included butterfish (4.8%), the sand lance, *Ammodytes* (<0.1%), and an unidentified member of the Cottidae (0.1%). Silver hake (<0.1%) were again identified as prey on Georges Bank but their contribution to the diet was insignificant. The only other fish identified were lanternfish, Myctophidae (3.2%), and the snakeblenny, *Lumpenus lumpretaeformis* (0.1%). Atlantic mackerel (28.0%); Atlantic herring (23.1%); alewife (9.4%); silver hake (1.4%); and butterfish (1.1%) were all preyed upon in the Gulf of Maine. In Western Nova Scotia the Gadidae (51.2%) were preyed on extensively but silver hake only composed 1.1% of the diet. None of the other fish were identified to species.

Crustacea formed the remaining bulk of the diet in all five geographic areas, and within this category the Euphausiacea and Pandalidae were the most important. In the Middle Atlantic, *Dichelopandalus* (8.2%) was the only pandalid shrimp identified. Most euphausiids (7.0%) were identified to the order level, however, those identified to the species level were found to be *Meganyctiphanes norvegica* (0.1%). The only other shrimp of any significance was *Crangon septemspinosa* (7.4%). *Dichelopandalus leptocerus* was also important in Southern New England and Georges Bank (8.6 and 1.8%, respectively), as were the euphausiids, *Meganyc-*

Table 1.—Geographic breakdown of food of the silver hake, *Merluccius bilinearis*, in the northwest Atlantic. Data are expressed as percentage weight, for fish collected during the spring and autumn bottom trawl survey cruises 1969-72. (+ indicates present but <0.1%.)

Prey	Middle Atlantic	Southern New England	Georges Bank	Gulf of Maine	Western Nova Scotia
POLYCHAETA	+	*1.1*	+	+	+
Nereidiformia	–	1.0	–	+	–
Terebelliformia	–	–	–	–	–
Sabelliformia	–	–	–	–	–
Other Polychaeta	+	0.1	+	+	+
CRUSTACEA	*27.7*	*33.6*	*20.4*	*21.5*	*33.8*
Amphipoda	1.0	1.3	0.1	+	+
Mysidacea	0.2	0.7	–	0.2	0.1
Euphausiacea	7.0	10.8	13.1	12.5	28.4
Pandalidae	8.5	15.7	2.6	1.7	0.4
Crangonidae	7.5	1.1	2.0	0.1	–
Axiidae	+	–	–	–	–
Paguridae	–	–	–	–	–
Majidae	–	–	–	–	–
Cancridae	0.1	–	+	0.1	–
Other Decapoda	0.7	1.3	0.7	4.8	0.2
Other Crustacea	2.7	2.7	1.9	2.1	4.7
MOLLUSCA	*13.6*	*0.8*	*0.6*	*1.3*	–
Gastropoda	+	–	–	–	–
Pelecypoda	+	–	–	+	–
Cephalopoda	13.6	0.8	0.6	1.3	–
Other Mollusca	+	–	–	–	–
ECHINODERMATA	–	–	+	–	–
Echinoidea	–	–	–	–	–
Ophiuroidea	–	–	+	–	–
Other Echinodermata	–	–	+	–	–
PISCES	*53.7*	*61.7*	*78.2*	*76.1*	*65.1*
Clupeidae	–	–	–	32.5	–
Gadidae	13.5	12.6	+	1.4	51.2
Scombridae	–	31.7	–	28.0	–
Scorpaenidae	–	–	–	–	–
Bothidae	–	–	–	–	–
Pleuronectidae	0.7	–	–	–	–
Other Pisces	39.5	17.4	78.2	14.2	13.9
Other groups	*0.1*	*0.2*	+	–	+
Animal remains	*4.9*	*2.6*	*0.8*	*1.1*	*1.1*
Sand and rock	+	+	+	+	+
Number of stomachs	465	704	248	453	282
Percentage of empty stomachs	34.6	35.8	24.6	30.7	33.3
Mean weight per stomach (g)	1.1	1.5	4.3	5.2	1.0
Mean predator fork length (cm)	26.7	27.5	29.9	27.1	27.7
Number of sampling stations	54	62	31	51	24

tiphanes (5.4 and 9.6%, respectively). In the Gulf of Maine, *Meganyctiphanes* was again the major crustacean prey (8.0%). The shrimp *Pasiphaea* (4.4%) replaced the pandalids, but *Dichelopandalus* (0.5%) and *Pandalus borealis* (0.3%) were still eaten in small quantities. In Western Nova Scotia euphausiids (28.4%), especially *Meganyctiphanes* (13.4%), were the only crustaceans of any significance.

The Mollusca were the only other taxonomic grouping to warrant discussion and here only in the Middle Atlantic. Cephalopods accounted for 13.6% of the diet with *Loligo* (8.3%) and *Rossia* (1.2%) being the two genera identified.

White hake, *Urophycis tenuis*.—White hake fed heavily on fish (Table 5). In Southern New England, silver hake (18.1%) and Atlantic mackerel (16.6%), were the most important prey, but "Other Pisces," such as the butterfish (2.8%) and wrymouth (1.7%), were also identified in the stomach contents. White hake taken from Georges Bank were also found to prey on silver hake (6.0%), but other gadids, such as red hake (7.7%), haddock (3.8%), and to a lesser degree, longfin hake (0.3%), were important. Clupeids represented almost half the fish eaten (27.7%), and of these almost half (12.1%) were identified as Atlantic herring. The Clupeidae also contributed heavily to the diet of white hake in the Gulf of Maine (17.5%) and at least part of the remains was identified as Atlantic herring (6.6%). Atlantic mackerel (9.6%) also accounted for some of the prey as did a number of fish in the "Other Pisces" category (47.2%). Some of these other fish were *Argentina silus* (16.6%); the wrymouth (1.1%); pearlsides (0.1%); and the sand lance, *Ammodytes* (0.1%). In Western Nova Scotia, Atlantic cod (2.2%), longfin hake (1.3%), and white hake (0.4%) contributed to the gadid prey. The redfish (4.7%),

Table 5.—Geographic breakdown of food of the white hake, *Urophycis tenuis*, in the northwest Atlantic. Data are expressed as percentage weight, for fish collected during the spring and autumn bottom trawl survey cruises 1969-72. (Middle Atlantic = no samples; + indicates present but <0.1%.)

Prey	Southern New England	Georges Bank	Gulf of Maine	Western Nova Scotia
POLYCHAETA	*0.1*	*0.1*	*0.1*	*0.3*
Nereidiformia	+	+	0.1	0.1
Terebelliformia	–	–	–	–
Sabelliformia	–	–	–	–
Other Polychaeta	0.1	0.1	+	0.2
CRUSTACEA	*3.7*	*29.4*	*21.1*	*10.4*
Amphipoda	0.3	0.1	+	0.1
Mysidacea	–	–	+	+
Euphausiacea	–	2.3	6.4	2.9
Pandalidae	0.5	21.7	10.7	4.3
Crangonidae	0.3	1.1	0.1	0.4
Axiidae	0.2	0.1	+	0.1
Paguridae	–	0.4	–	+
Majidae	–	–	–	–
Cancridae	1.8	0.4	–	–
Other Decapoda	0.6	1.9	3.0	1.9
Other Crustacea	+	1.4	0.9	0.7
MOLLUSCA	*11.6*	*3.8*	*0.2*	*0.4*
Gastropoda	+	+	+	–
Pelecypoda	–	+	+	–
Cephalopoda	11.6	3.5	0.2	0.4
Other Mollusca	–	0.3	–	+
ECHINODERMATA	–	–	+	–
Echinoidea	–	–	–	–
Ophiuroidea	–	–	+	–
Other Echinodermata	–	–	–	–
PISCES	*83.3*	*62.5*	*76.5*	*86.5*
Clupeidae	–	27.6	17.5	0.8
Gadidae	18.1	17.8	1.1	25.7
Scombridae	16.6	–	9.6	–
Scorpaenidae	–	–	1.1	4.7
Bothidae	–	–	–	–
Pleuronectidae	–	–	–	–
Other Pisces	48.6	17.1	47.2	55.3
Other groups	*0.1*	+	*0.1*	+
Animal remains	*1.2*	*4.0*	*2.0*	*2.3*
Sand and rock	–	*0.2*	+	*0.1*
Number of stomachs	95	173	475	169
Percentage of empty stomachs	26.3	23.1	27.4	13.4
Mean weight per stomach (g)	22.5	10.0	18.5	22.6
Mean predator fork length (cm)	48.3	45.3	46.5	43.7
Number of sampling stations	24	38	74	41

Table 6.—Geographic breakdown of food of the offshore hake, *Merluccius albidus*, in the northwest Atlantic. Data are expressed as percentage weight, for fish collected during the spring and autumn bottom trawl survey cruises 1969-72. (Gulf of Maine and Western Nova Scotia = no samples; + indicates present but <0.1%.)

Prey	Middle Atlantic	Southern New England	Georges Bank
POLYCHAETA	–	–	–
Nereidiformia	–	–	–
Terebelliformia	–	–	–
Sabelliformia	–	–	–
Other Polychaeta	–	–	–
CRUSTACEA	*100.0*	*3.2*	*14.0*
Amphipoda	–	–	–
Mysidacea	–	–	–
Euphausiacea	62.5	0.8	1.5
Pandalidae	–	1.6	6.4
Crangonidae	–	–	–
Axiidae	–	–	–
Paguridae	–	–	–
Majidae	–	–	–
Cancridae	–	–	–
Other Decapoda	37.5	0.8	6.1
Other Crustacea	–	–	–
MOLLUSCA	–	–	5.1
Gastropoda	–	–	–
Pelecypoda	–	–	–
Cephalopoda	–	–	5.1
Other Mollusca	–	–	–
ECHINODERMATA	–	–	–
Echinoidea	–	–	–
Ophiuroidea	–	–	–
Other Echinodermata	–	–	–
PISCES	–	*96.7*	*80.4*
Clupeidae	–	–	–
Gadidae	–	73.8	–
Scombridae	–	–	–
Scorpaenidae	–	–	–
Bothidae	–	–	–
Pleuronectidae	–	–	–
Other Pisces	–	22.9	80.4
Other groups	–	+	–
Animal remains	–	*0.1*	*0.5*
Sand and rock	–	–	–
Number of stomachs	4	46	23
Percentage of empty stomachs	25.0	58.7	60.9
Mean weight per stomach (g)	0.1	3.1	1.4
Mean predator fork length (cm)	31.3	30.9	37.1
Number of sampling stations	2	9	3

sand lance (2.9%), and longhorn sculpin (0.2%), are most of the other fish that were identified.

Crustacea was generally the second most important taxonomic grouping except in Southern New England where Cephalopods (11.6%) such as *Loligo* (6.5%) were preyed on. In the Gulf of Maine and on Georges Bank three species of pandalid shrimp were eaten, *Dichelopandalus leptocerus* (0.1% in the Gulf of Maine and 3.5% on Georges Bank), *Pandalus borealis* (3.9% in the Gulf of Maine and 0.4% on Georges Bank), and *P. montagui* (0.5% in the Gulf of Maine and 0.2% on Georges Bank). In Western Nova Scotia *P. propinquus* (0.2%) was also present but *P. borealis* was not. The only other crustaceans of note were euphausiids, and these primarily in the Gulf of Maine, where *Meganyctiphanes* (3.5%) was the most important species.

Offshore hake, *Merluccius albidus*.—Stomachs were collected from offshore hake in three of the five geographic areas (Table 6). In the Middle Atlantic, data were collected from only four fish, and therefore a discussion of the food in this area is of little value. Suffice it to say that the two species of Crustacea eaten, *Meganyctiphanes norvegica* and *Pasiphaea* sp., were also preyed upon in the other geographic areas. In Southern New England and on Georges Bank, the composition of the diet was very similar. In both areas fish was the major prey group (96.7% in Southern New England and 80.4% on Georges Bank); however, the particular species of fish could not be identified. Crustaceans were of secondary

importance, with *Dichelopandalus leptocerus* (1.5% in Southern New England and 6.4% on Georges Bank) being the main prey item within this group.

Cusk, *Brosme brosme*.—The areal breakdown of food for cusk (Table 7) differs significantly from the summary (Table 1) which combines all areas into a single group. This is primarily due to the heavy predation on fish in Western Nova Scotia (98.2% of the diet). In the three other areas where cusk were collected the major prey was either crustaceans or echinoderms. On Georges Bank only four fish were examined and, of the two which had food in their stomachs, the prey was either brittle stars (80.0%) or the toad crab, *Hyas coarctatus* (20.0%). In Southern New England very few fish were examined. The total quantity of prey was extremely small and consisted exclusively of amphipods, Aoridae (57.1%) and Gammaridae (42.9%). The largest sample of cusk came from the Gulf of Maine, and here the primary prey was Crustacea (90.6%). Of the decapods that could be identified, the three pandalids, *Pandalus borealis* (17.0%), *Dichelopandalus leptocerus* (3.5%), and *P. propinquus* (0.5%), together with some penaeid shrimp (6.9%), were the most important. However, small quantities of *Meganyctiphanes norvegica* (1.7%) were also found in the stomach contents. The remainder of the diet consisted of fish (4.2%), and "Other Groups" such as brachiopods (1.2%), and sand or animal remains (3.9%).

Table 7.—Geographic breakdown of food of the cusk, *Brosme brosme*, in the northwest Atlantic. Data are expressed as percentage weight, for fish collected during the spring and autumn bottom trawl survey cruises 1969-72. (Middle Atlantic = no samples; + indicates present but <0.1%.)

Prey	Southern New England	Georges Bank	Gulf of Maine	Western Nova Scotia
POLYCHAETA	–	–	–	–
Nereidiformia	–	–	–	–
Terebelliformia	–	–	–	–
Sabelliformia	–	–	–	–
Other Polychaeta	–	–	–	–
CRUSTACEA	*100.0*	*20.0*	*90.6*	*1.4*
Amphipoda	100.0	–	–	–
Mysidacea	–	–	–	–
Euphausiacea	–	–	1.7	–
Pandalidae	–	–	21.0	–
Crangonidae	–	–	–	–
Axiidae	–	–	–	–
Paguridae	–	–	–	–
Majidae	–	20.0	–	–
Cancridae	–	–	–	–
Other Decapoda	–	–	55.5	1.1
Other Crustacea	–	–	12.4	0.3
MOLLUSCA	–	–	–	–
Gastropoda	–	–	–	–
Pelecypoda	–	–	–	–
Cephalopoda	–	–	–	–
Other Mollusca	–	–	–	–
ECHINODERMATA	–	*80.0*	–	–
Echinoidea	–	–	–	–
Ophiuroidea	–	80.0	–	–
Other Echinodermata	–	–	–	–
PISCES	–	–	*4.2*	98.2
Clupeidae	–	–	–	–
Gadidae	–	–	–	–
Scombridae	–	–	–	–
Scorpaenidae	–	–	–	–
Bothidae	–	–	–	–
Pleuronectidae	–	–	–	–
Other Pisces	–	–	4.2	98.2
Other groups	–	–	*1.3*	–
Animal remains	–	–	*3.1*	*0.4*
Sand and rock	–	–	*0.8*	–
Number of stomachs	6	4	51	11
Percentage of empty stomachs	33.3	50.0	78.4	81.8
Mean weight per stomach (g)	0.01	4.89	0.88	15.03
Mean predator fork length (cm)	25.5	57.3	64.8	60.5
Number of sampling stations	1	4	29	9

Red hake, *Urophycis chuss*.—In all five geographic areas, at least half the red hake's diet was composed of crustaceans (Table 8). In the Middle Atlantic, munid crabs of the genera *Munida* (16.9%) and *Munidopsis* (3.3%) accounted for a large percentage of the crustaceans classified under "Other Decapoda." Pandalid shrimp (15.7%) were the next most important prey group with the majority of these identified as *Dichelopandalus* (9.1%). Of secondary importance were the unidentified amphipods (5.1%); the rock crab, *Cancer irroratus* (2.6%); the sand shrimp, *Crangon* (2.2%); and the isopod, *Cirolina* (1.8%). In Southern New England the munid crab, *Munida* (12.9%), was again of primary importance, as was *Dichelopandalus* (5.6%). *Cancer irroratus* (1.6%) and *Crangon* (1.5%) were also preyed upon. On Georges Bank the hermit crab, *Pagurus* (10.6%), and the sand shrimp, *Crangon* (20.6%), were major prey items. *Cancer* crabs (8.7%) and pandalid shrimp, *Dichelopandalus* (6.1%), also contributed significantly to the diet. Euphausiids (18.7%), some of which could be identified as *Meganyctiphanes* (5.6%); the pandalid shrimp, *Dichelopandalus* (11.6%); and the crab *Cancer* (11.2%), were of major importance in the Gulf of Maine, while the pandalids, *Dichelopandalus leptocerus* (30.9%) and *Pandalus montagui* (40.3%), were the primary prey in Western Nova Scotia.

In three of the geographic areas, Pisces followed the Crustacea as a major prey category. Many of the fish eaten in the Middle Atlantic could not be identified. However, of those identified one of the "Other Pisces" was the snake eel (5.9%), and the pleuronectid was the winter flounder (0.1%). Red hake were cannibalistic in Southern New England (0.3%) but also ate other gadids such as the silver hake (0.3%). The wrymouth (1.8%), Gulf Stream flounder (0.9%), and the Atlantic mackerel (0.6%) made up a small percentage of the other fish eaten. On Georges Bank clupeids (3.5%) and "Other Pisces" (1.8%) accounted for all the fish prey. Fish remains (23.9%) from the stomachs of red hake caught in the Gulf of Maine could not be identified.

Table 8.—Geographic breakdown of food of the red hake, *Urophycis chuss*, in the northwest Atlantic. Data are expressed as percentage weight, for fish collected during the spring and autumn bottom trawl survey cruises 1969-72. (+ indicates present but <0.1%.)

Prey	Middle Atlantic	Southern New England	Georges Bank	Gulf of Maine	Western Nova Scotia
POLYCHAETA	*1.4*	*3.3*	*3.0*	*2.9*	*2.4*
Nereidiformia	0.1	1.7	1.1	0.6	0.4
Terebelliformia	–	–	0.2	–	–
Sabelliformia	–	0.2	+	–	–
Other Polychaeta	1.3	1.4	1.7	2.3	2.0
CRUSTACEA	*52.2*	*50.8*	*57.2*	*64.7*	*88.5*
Amphipoda	5.5	9.6	4.3	1.8	1.9
Mysidacea	0.1	+	+	0.6	0.2
Euphausiacea	+	1.8	2.0	18.7	2.3
Pandalidae	15.7	9.4	7.7	19.7	71.2
Crangonidae	2.2	1.5	10.6	0.6	1.9
Axiidae	–	2.9	1.9	–	–
Paguridae	0.5	1.3	10.6	2.3	3.2
Majidae	+	0.1	–	–	–
Cancridae	2.7	4.4	8.7	11.2	
Other Decapoda	21.7	15.5	3.0	4.4	7.6
Other Crustacea	3.8	4.3	8.4	5.4	0.2
MOLLUSCA	*0.3*	*5.4*	*17.7*	*3.8*	–
Gastropoda	0.2	0.1	17.4	3.8	–
Pelecypoda	0.1	+	–	–	–
Cephalopoda	–	2.2	–	–	–
Other Mollusca	+	3.1	0.3	–	–
ECHINODERMATA	*0.1*	*0.6*	*0.2*	*2.0*	–
Echinoidea	–	0.1	0.2	–	–
Ophiuroidea	–	–	–	–	–
Other Echinodermata	0.1	0.5	+	2.0	–
PISCES	*38.5*	*28.2*	*5.3*	*23.9*	*0.6*
Clupeidae	–	–	3.5	–	–
Gadidae	–	0.7	–	–	–
Scombridae	–	0.6	–	–	–
Scorpaenidae	–	–	–	–	–
Bothidae	–	0.9	–	–	–
Pleuronectidae	0.1	–	–	–	–
Other Pisces	38.4	26.0	1.8	23.9	0.6
Other groups	+	*1.2*	*0.2*	*0.1*	*5.4*
Animal remains	*7.2*	*10.3*	*16.2*	*2.5*	*2.9*
Sand and rock	*0.3*	*0.2*	*0.2*	*0.1*	*0.2*
Number of stomachs	206	607	208	72	17
Percentage of empty stomachs	16.4	13.3	21.6	19.4	11.8
Mean weight per stomach (g)	1.8	2.4	1.9	2.9	2.6
Mean predator fork length (cm)	29.3	29.6	33.1	34.3	32.6
Number of sampling stations	25	71	30	20	8

The only other taxon that was of any significance, and then only on Georges Bank, was the Mollusca of the class Gastropoda (17.4%).

Spotted hake, *Urophycis regius*.—The areal breakdown of food of the spotted hake is limited to the Middle Atlantic and Southern New England, since no stomachs were collected in the Gulf of Maine and Western Nova Scotia, and only four fish were analyzed from Georges Bank (Table 9). A comparison between the two areas showed that the foods were reasonably similar, the major difference being due to the importance of cephalopods (16.1%), especially *Loligo* (6.8%), in the Middle Atlantic.

Crustaceans were a major prey category. In both the Middle Atlantic and Southern New England the "Other Decapoda" was the largest grouping consisting mostly of the munid crabs. In the Middle Atlantic, *Munida* (9.4%), both *M. iris* (7.4%) and *M. valida* (1.7%), together with *Munidopsis* (2.8%), were present in the stomach contents, but in Southern New England the species were restricted to *M. iris* (11.3%) and *M. valida* (9.2%). Interestingly, hyperiid amphipods were important, making up 3.4% of the diet in the Middle Atlantic and 6.1% in Southern New England. The rock crab, *Cancer irroratus* (6.7%), composed a significant part of the prey in the Middle Atlantic. Other crustaceans of secondary importance were *Crangon* (4.8% in the Middle Atlantic and 2.6% in Southern New England), *Dichelopandalus* (3.6% in the Middle Atlantic and 4.0% in Southern New England), and the isopods (3.1% in the Middle Atlantic only), such as *Cirolina polita* (0.7%), which are included under "Other Crustacea."

"Pisces" was the last major grouping. In the Middle Atlantic, red hake (3.4%) and silver hake (3.3%); the bothid, *Citharichthys arctifrons* (1.7%); the pleuro-

Table 9.—Geographic breakdown of food of the spotted hake, *Urophycis regius*, in the northwest Atlantic. Data are expressed as percentage weight, for fish collected during the spring and autumn bottom trawl survey cruises 1969-72. (Gulf of Maine and Western Nova Scotia = no samples; + indicates present but <0.1%.)

Prey	Middle Atlantic		Southern New England		Georges Bank	
POLYCHAETA	*0.4*		*0.6*		–	
Nereidiformia		0.1		0.1		–
Terebelliformia		–		–		–
Sabelliformia		–		–		–
Other Polychaeta		0.3		0.5		–
CRUSTACEA	*48.6*		*46.8*		*6.8*	
Amphipoda		8.0		6.2		2.9
Mysidacea		+		–		–
Euphausiacea		+		0.1		–
Pandalidae		3.8		4.3		–
Crangonidae		5.0		2.6		1.2
Axiidae		–		0.1		–
Paguridae		0.1		0.1		–
Majidae		+		–		–
Cancridae		10.3		1.1		–
Other Decapoda		14.5		31.9		0.3
Other Crustacea		6.9		0.4		2.4
MOLLUSCA	*16.6*		*1.1*		*71.6*	
Gastropoda		0.1		–		–
Pelecypoda		0.4		–		–
Cephalopoda		16.1		1.0		71.6
Other Mollusca		+		0.1		–
ECHINODERMATA	–		+		–	
Echinoidea		–		–		–
Ophiuroidea		–		–		–
Other Echinodermata		–		+		–
PISCES	*28.5*		*45.1*		*0.3*	
Clupeidae		–		–		–
Gadidae		6.8		0.3		–
Scombridae		–		9.1		–
Scorpaenidae		–		–		–
Bothidae		1.7		1.9		–
Pleuronectidae		0.8		0.8		–
Other Pisces		19.2		33.0		0.3
Other groups	+		*0.1*		+	
Animal remains	*5.7*		*5.8*		*21.3*	
Sand and rock	*0.2*		*0.5*		+	
Number of atomachs	689		183		4	
Percentage of empty stomachs	10.5		31.0		25.0	
Mean weight per stomach (g)	0.8		1.9		2.8	
Mean predator fork length (cm)	18.2		26.2		24.1	
Number of sampling stations	45		17		2	

nectid, *Limanda ferruginea* (0.8%); and "Other Pisces" (19.2%) such as the snake eel (0.2%), and lanternfish (family Myctophidae) (3.9%), constituted the fish prey. In Southern New England the fawn cusk-eel (1.1%) and some unidentified cusk eels (10.8%), together with Atlantic mackerel (9.1%), the Gulf Stream flounder (1.9%), and silver hake (1.1%), represented a large part of the fish consumed.

Haddock, *Melanogrammus aeglefinus*.—Few haddock were collected in the Middle Atlantic and Southern New England and therefore the following discussion is limited primarily to the three other geographic areas (Table 10).

Fish accounted for more than one-fourth (28.4%) of the haddock's diet on Georges Bank whereas fish were reasonably insignificant in all the other areas. This shift in food was not, however, due to a change in feeding strategy but rather was entirely due to the consumption of herring eggs. This implies that haddock prey heavily on herring spawn when it is available. Polychaetes were also more important prey on Georges Bank (23.5%) than in the other areas. The "Other Polychaeta" category contributed the largest percentage (18.3%) with *Ammotrypane aulogaster* (8.3%) being the most important animal. *Laonice* (0.1%), *Ophelia* (<0.1%), *Scalibregma* (<0.1%), and *Sternaspis* (0.1%) were other polychaetes identified in the stomach contents. None of the Terebelliformia (2.1%) could be identified below suborder and *Chone infundibuliformis* (0.3%) was the only Sabelliformia (2.1%) identified to species. The third prey group that was of any significance was the crustaceans (16.0%). Amphipods (7.1%) made up the largest portion but the individual species of amphipods usually accounted for <0.1%. As a group the gammarid amphipods were the most important, with species such as *Unciola irrorata* (<0.1%), *Casco bigelowi* (<0.1%), *Anonyx* sp. (0.1%), *Leptocerus pinguis* (0.1%), and *Pleustes* sp. (<0.1%) having been found in the haddock stomachs. Echinoderms (7.8%) and molluscs (3.8%) were the least important prey groups for Georges Bank haddock. Brittle stars, such as *Ophiopholis aculeata* (2.4%), were the most important echinoderms, while pelecypods like *Astarte* (0.2%) and *Pecten* (0.1%) were the more important molluscs that could be identified. Sand and rocks (15.3%) were more prevalent in the haddock stomachs collected on Georges Bank than elsewhere, possibly because polychaetes and pelecypods accounted for a larger percentage of the diet here than in the other areas.

The haddock's food in the Gulf of Maine and Western Nova Scotia were quite different from those in the other three geographic areas, but within these two areas the prey was similar. For example, in both areas half the diet consisted of echinoderms. Similarly, crustaceans and polychaetes contributed between 10 and 15% of the diet and molluscs between 1 and 3%. Brittle stars were the main food item, with *Ophiura* (16.2%) being of primary importance in the Gulf of Maine. However, *Amphiura* (0.8%), *Ophiopholis* (0.4%), and *Ophiacantha bidentata* (<0.1%), together with unidentified ophiuroid remains (20.5%), are also included in this prey group. In Western Nova Scotia three ophiuroids were eaten, *Ophiopholis* (13.0%), *Ophiura* (8.2%), and *Amphiopolis* (0.2%), together with some unidentifiable ophiuroid remains (13.0%). In the Gulf of Maine 15.2% of the diet was crustaceans. The "Other Decapoda" was the largest group (5.9%) primarily because of the shrimp *Pasiphaea* (4.9%). The shrimp *Pandalus* (2.0%) was of secondary importance as were euphausiids (1.9%) and gammarid amphipods (1.8%). Gammarid amphipods (3.4%) as well as the caprellid; *Aeginina longicornis* (0.3%), were the main crustacean prey in Western Nova Scotia, while the Axiide, both *Axius* (1.8%) and *Calocaris* (0.5%), were of secondary importance. Polychaetes were the only other group accounting for much of the diet. The majority were not identified below the order level, but in the Gulf of

Table 10.—Geographic breakdown of food of haddock, *Melanogrammus aeglefinus*, in the northwest Atlantic. Data are expressed as percentage weight, for fish collected during the spring and autumn bottom trawl survey cruises 1969-72. (+ indicates present but <0.1%.)

Prey	Middle Atlantic	Southern New England	Georges Bank	Gulf of Maine	Western Nova Scotia
POLYCHAETA	*14.3*	*4.5*	*23.5*	*14.7*	*11.8*
Nereidiformia	13.4	2.5	1.0	3.0	2.7
Terebelliformia	–	–	2.1	+	1.9
Sabelliformia	–	–	2.1	0.5	0.8
Other Polychaeta	0.9	2.0	18.3	11.2	6.4
CRUSTACEA	*2.2*	*82.0*	*16.0*	*15.2*	*14.4*
Amphipoda	0.6	75.3	7.1	2.2	5.0
Mysidacea	–	–	0.1	–	+
Euphausiacea	–	–	3.7	2.0	1.7
Pandalidae	–	0.7	1.1	2.9	1.0
Crangonidae	0.3	0.5	0.2	–	0.1
Axiidae	–	–	0.2	0.2	2.3
Paguridae	–	0.9	0.2	0.1	0.8
Majidae	–	0.6	0.1	0.5	0.4
Cancridae	–	0.2	0.2	–	–
Other Decapoda	–	1.0	0.2	5.9	1.7
Other Crustacea	1.3	2.8	2.9	1.4	1.4
MOLLUSCA	*0.4*	*0.7*	*3.8*	*1.6*	*3.0*
Gastropoda	0.4	+	0.2	0.5	0.3
Pelecypoda	–	0.7	3.2	0.9	1.9
Cephalopoda	–	+	0.1	–	0.5
Other Mollusca	–	–	0.3	0.2	0.3
ECHINODERMATA	–	*1.4*	*7.8*	*51.9*	*49.0*
Echinoidea	–	1.2	1.5	10.6	9.0
Ophiuroidea	–	+	6.0	38.0	34.5
Other Echinodermata	–	0.2	0.3	3.3	5.5
PISCES	–	+	*28.4*	*2.2*	*3.8*
Clupeidae	–	–	28.3	–	–
Gadidae	–	–	–	–	0.8
Scombridae	–	–	–	–	–
Scorpaenidae	–	–	–	–	–
Bothidae	–	–	–	–	–
Pleuronectidae	–	–	+	–	–
Other Pisces	–	+	0.1	2.2	3.0
Other groups	*1.1*	*0.1*	*0.3*	*0.6*	*2.0*
Animal remains	–	*8.3*	*4.9*	*11.2*	*13.0*
Sand and rock	*82.0*	*3.0*	*15.3*	*2.6*	*3.0*
Number of stomachs	10	27	352	232	510
Percentage of empty stomachs	0.0	11.1	4.3	5.6	10.0
Mean weight per stomach (g)	3.2	4.1	10.0	6.6	4.9
Mean predator fork length (cm)	20.1	54.8	46.7	56.3	43.4
Number of sampling stations	1	5	45	47	56

Maine some of the more common were *Sabella* (0.4%), *Eunice pennata* (0.2%), *Nephtys* (0.2%), *Goniada* (0.1%), and *Lumbrineris* (0.1%). In Western Nova Scotia a variety of polychaetes were identified in the stomach contents but the only genera contributing >0.1% to the diet were *Cistenides* (0.5%), *Aphrodita* (0.8%), and *Eunice* (0.4%).

Longfin hake, *Phycis chesteri*.—Although longfin hake were collected in all five geographic areas, a discussion of the areal breakdown of its prey is of little value. Few fish were collected and, on Georges Bank, where the largest sample was taken, over half the stomachs were empty, effectively leaving a maximum of 26 fish from 6 stations to evaluate the food in any one region. Nevertheless, in all areas, crustaceans were the major prey, with the euphausiid, *Meganyctiphanes norvegica*, being the most important.

Fourbeard rockling, *Enchelyopus cimbrius*.—Fourbeard rockling were collected for stomach contents analysis in three of the five geographic areas. Only on Georges Bank, however, was the total weight of the prey (12.42 g) and sample size (n = 27) sufficiently large to warrant any discussion. On Georges Bank crustaceans were the major prey, accounting for 59.3% of the diet. The two most important crustaceans were *Crangon septemspinosa* (46.3%) and *Dichelopandalus leptocerus* (11.2%). The other taxonomic grouping of importance was the Polychaeta (13.6%), and here the only identification to the genus level was *Ammotrypane* (3.9%).

Marlin-spike, *Nezumia bairdi*.—Marlin-spike were collected in three of the geographic areas, Southern New England, Gulf of Maine, and Western Nova Scotia, but in very small numbers. Due to the small sample size, both in the number of fish examined and the total weight

of prey, a meaningful discussion of areal differences in food is unwarranted. Table 2 adequately summarizes the available information.

Longnose grenadier, *Coelorhynchus carminatus*.—As has been described for the marlin-spike, a meaningful discussion of the areal differences in food is not justifiable because of the small number of fish examined and the small quantity of prey in the stomachs.

Fawn cusk-eel, *Lepophidium cervinum*.—Fawn cusk-eel were collected in significant numbers in the Middle Atlantic and Southern New England but the total quantity of prey in the stomachs amounted to only 3.27 g. An areal breakdown of their food is therefore of little value, especially since almost 1 g of the total weight was due to a heavy infestation of parasitic nematodes (37.1%) in the fish collected in the Middle Atlantic. For a summary of the food see Table 2.

Ocean pout, *Macrozoarces americanus*.—Ocean pout were collected in all areas but were most abundant in Southern New England and on Georges Bank (Table 11). In these two areas the major prey was echinoderms, with the sand dollar being the single most important species (54.4% in Southern New England and 61.6% on Georges Bank). In Southern New England, crustaceans (22.0%) and polychaetes (7.8%) made up most of the remainder of the prey. Amphipods (13.1%), such as *Unciola* sp. (1.0%) and *Leptocerus pinguis* (1.2%), were important, as were the rock crabs (5.4%), particularly *Cancer irroratus* (2.0%). The majority of the polychaete prey was identified as *Aphrodita* (7.4%). On Georges Bank, crustaceans (4.3%) were of little significance and

Table 11.—Geographic breakdown of food of ocean pout, *Macrozoarces americanus*, in the northwest Atlantic. Data are expressed as percentage weight, for fish collected during the spring and autumn bottom trawl survey cruises 1969-72. (+ indicates present but <0.1%.)

Prey	Middle Atlantic	Southern New England	Georges Bank	Gulf of Maine	Western Nova Scotia
POLYCHAETA	–	*7.8*	*0.5*	*0.3*	–
Nereidiformia	–	7.7	+	–	–
Terebelliformia	–	–	+	+	–
Sabelliformia	–	–	–	–	–
Other Polychaeta	–	0.1	0.5	0.3	–
CRUSTACEA	*9.4*	*22.0*	*4.3*	*3.5*	+
Amphipoda	0.2	13.1	0.7	2.0	–
Mysidacea	–	–	–	–	–
Euphausiacea	–	–	–	–	–
Pandalidae	–	+	+	–	–
Crangonidae	–	+	+	0.2	–
Axiidae	–	–	–	–	–
Paguridae	0.3	0.1	0.8	0.3	–
Majidae	–	–	0.7	–	–
Cancridae	5.7	5.4	1.3	0.1	–
Other Decapoda	–	1.3	0.7	–	–
Other Crustacea	3.2	2.1	0.1	0.9	+
MOLLUSCA	–	*1.6*	*6.1*	*4.1*	–
Gastropoda	–	0.9	0.1	2.0	–
Pelecypoda	–	0.6	5.9	2.1	–
Cephalopoda	–	–	–	–	–
Other Mollusca	–	0.1	0.1	–	–
ECHINODERMATA	*86.3*	*63.9*	*81.1*	*37.2*	*99.3*
Echinoidea	86.3	63.9	71.5	25.3	–
Ophiuroidea	–	+	9.6	6.2	99.3
Other Echinodermata	–	–	–	5.7	–
PISCES	*0.5*	*0.1*	+	*0.5*	+
Clupeidae	–	–	–	–	–
Gadidae	–	–	–	–	–
Scombridae	–	–	–	–	–
Scorpaenidae	–	–	–	–	–
Bothidae	–	–	–	–	–
Pleuronectidae	–	–	–	–	–
Other Pisces	0.5	0.1	+	0.5	+
Other groups	*0.2*	*0.3*	*1.9*	*18.5*	–
Animal remains	*1.8*	*2.5*	*5.4*	*2.5*	–
Sand and rock	*1.8*	*1.8*	*0.7*	*33.4*	*0.7*
Number of stomachs	20	207	110	34	6
Percentage of empty stomachs	0.0	22.5	32.7	26.5	66.7
Mean weight per stomach (g)	6.6	5.0	10.6	6.4	0.5
Mean predator fork length (cm)	44.7	45.2	56.5	36.6	32.4
Number of sampling stations	4	23	31	4	3

ophiuroids (9.6%), such as *Ophiopholis* (1.1%), and the pelecypod, *Pecten* (4.5%), formed the remaining bulk of the diet. In the Middle Atlantic few ocean pout were collected, but as on Georges Bank and in Southern New England, the single major prey species was the sand dollar (86.3%). In the Gulf of Maine echinoderms were apparently less important although *E. parma* still accounted for 24.8% of the prey. "Other Groups" was also important and the single contributor to this category was the tunicate, *Cnemidocarpa mollis* (18.5%). Sand and rock (33.4%) made up a large part of the weight of the stomach contents.

Dietary Overlap

The percentage similarity values (Fig. 3) calculated from the data in Table 2 range from 1 to a maximum of 75. In order to facilitate the comparison between species, similarity values have been grouped into three categories representing low (0 to <30%), intermediate (30 to <60%), and high (60 to 100%) levels of dietary overlap. Accordingly, it is obvious that the greatest similarity in diet exists between the silver and white hake (75%), the marlin-spike and longnose grenadier (75%), the red and spotted hake (71%), and the pollock and silver hake (63%).

The diets of Atlantic cod, pollock, silver hake, white hake, offshore hake, cusk, red hake, and spotted hake are reasonably similar. Most of these fish populations are primarily piscivorous, which accounts for the observed intermediate and high levels of dietary overlap. The red and spotted hake, however, qualify as "mixed feeders" preying on both fish and invertebrates. In contrast to the eight predators listed above, the remaining seven species: haddock, longfin hake, fourbeard rockling, marlin-spike, longnose grenadier, fawn cusk-eel, and ocean pout, prey almost exclusively on invertebrates. Of these fish only the haddock preyed extensively on other fish and this was predation on herring eggs rather than on juvenile or adult fishes. The lack of similarity between the diet of the invertebrate feeders is in part due to the more numerous categories of potential prey. In some instances, such as for the marlin-spike, longnose grenadier, and fourbeard rockling, estimates of diet similarly are of limited value because of the small number of fish examined and/or the small amount of prey found in the stomachs.

The percentage similarity in diet has also been calculated for each fish in the five individual geographic

	Atlantic Cod	Pollock	Silver Hake	White Hake	Offshore Hake	Cusk	Red Hake	Spotted Hake	Haddock	Longfin Hake	Fourbeard Rockling	Marlin-spike	Longnose Grenadier	Fawn Cusk-eel	Ocean Pout
Atlantic Cod															
Pollock	59														
Silver Hake	58	63													
White Hake	57	52	75												
Offshore Hake	33	32	44	51											
Cusk	37	42	41	55	39										
Red Hake	53	45	44	45	31	44									
Spotted Hake	51	43	47	44	34	44	71								
Haddock	34	25	26	24	7	16	33	21							
Longfin Hake	13	53	25	18	7	21	32	26	10						
Fourbeard Rockling	13	10	13	16	6	11	31	21	27	16					
Marlin-spike	13	14	7	6	2	16	37	40	35	25	41				
Longnose Grenadier	9	13	6	6	2	14	27	28	26	18	48	75			
Fawn Cusk-eel	11	8	10	7	3	7	30	23	30	16	45	44	41		
Ocean Pout	18	5	5	5	1	9	19	16	34	3	7	15	9	17	

0 < 30 | 30 < 60 | 60 < 100

Figure 3.—Percentage similarity between the diet of 15 species of gadiform fishes from the northwest Atlantic. For calculation methods, see text. Open boxes = 0 to <30%; ruled boxes = 30 to <60%; solid boxes = 60 to 100%.

areas. The 15 species of fish were not omnipresent and the data were only included in the calculations if 10 or more individuals of that particular species were collected in a geographic area for stomach contents analysis.

Only 6 of the 15 predators were collected in sufficiently large numbers in the Middle Atlantic to warrant an analysis of dietary overlap. Three of these six fish—silver, red, and spotted hake—showed intermediate levels of dietary overlap, while the similarity in diet for the haddock, fawn cusk-eel, and ocean pout was low.

In Southern New England 10 of the 15 predators were present. A high degree of similarity in diet occurred between the red and spotted hake. These two fish fed on both fish and invertebrates, and shared many of the same species as prey (Tables 8, 9). Intermediate levels of dietary overlap were generally found between the four piscivorous predators, Atlantic cod, silver hake, white hake, and offshore hake, and also between these same four fish and the red and spotted hake. The only other intermediate levels of overlap occurred between the fawn cusk-eel and the red hake and haddock. Little similarity was found between the diet of the haddock, longfin hake, fawn cusk-eel, ocean pout, and the other more piscivorous predators mentioned above.

For the fish taken on Georges Bank high levels of dietary overlap occurred between the offshore and silver hake and between the pollock and longfin hake. The high overlap between the pollock, which have normally been considered piscivorous, and the longfin hake, an invertebrate feeder, may be explained by the dependence on Crustacea as a major food source for Georges Bank pollock (Table 3). It should also be noted that the average length of pollock on Georges Bank was smaller than in the other geographic areas which might explain the reliance on crustaceans rather than fish. Intermediate levels of diet similarity were found for a number of fish. Most notable is the overlap between Atlantic cod and haddock which may be traced to the heavy predation on herring eggs by the Georges Bank haddock. Since Atlantic cod were preying on either juvenile or adult herring, this measure of overlap is somewhat misleading. Low levels of similarity were again observed between the invertebrate feeders.

In the Gulf of Maine high and intermediate levels of dietary overlap were found between the Atlantic cod, pollock, silver hake, white hake, and red hake, but little similarity was observed between the diet of these same predators and the haddock, longfin hake, fourbeard rockling, and ocean pout. The cusk showed an intermediate level of dietary overlap with the pollock, red hake, and fourbeard rockling while the diet of the ocean pout was found to have an intermediate degree of similarity with the haddock. All the remaining fish showed a low level of dietary overlap.

In Western Nova Scotia the highest level of dietary overlap was found between the Atlantic cod and white hake. Intermediate overlap was generally found between the diets of the Atlantic cod, pollock, silver hake, white hake, and cusk. Longfin hake also showed an intermediate level of overlap with the pollock, silver hake, and marlin-spike. The last intermediate level occurred between the marlin-spike and haddock. Little similarity in diet was found for the other gadiform fish collected on the Scotian Shelf.

DISCUSSION

Food

Atlantic cod.—Data on the diet of the Atlantic cod occurring off the U.S. coast in the Gulf of Maine have been summarized by Bigelow and Schroeder (1953) (see also Wise 1961), but, surprisingly, there is little other information for the region of the present study (e.g., Kendall 1898; Tyler 1972). The Canadian cod stocks in the Gulf of St. Lawrence and off Newfoundland have, however, been more thoroughly investigated (Powles 1958; Popova 1962; Templeman 1965; Kohler and Fitzgerald 1969; Minet and Perodou 1978).

From some of the earliest studies it was concluded that Atlantic cod will eat almost any food available. Despite a wide diversity in the species composition of the diet, a rather simple picture of the cod's food habits may be drawn from most of the available data. In general, crustaceans and fish are the major prey, while the actual percentage of the diet made up of each of these two taxonomic groups is determined by prey size and prey availability. Small cod prey on small crustaceans, such as amphipods and mysids. Slightly larger cod prey more on decapod crabs and shrimp. The larger cod prey almost exclusively on fish. Our observations on the food of Atlantic cod caught off the U.S. coast are in agreement with this rather simplistic description. Although we did not separate the data into size classes, it can be seen that fish and crustaceans were the most important prey categories (Table 1). We did not include the smaller cod (<20 cm) in our data base, and the average length of the 1,541 animals we analyzed was 54.7 cm (Table 1). Cod of approximately 50 cm FL (fork length) have previously been shown to prey heavily on both fish and crustaceans (Powles 1958; Popova 1962; Rae 1968) so that our data may be taken as confirmation that the diet of the U.S. cod stocks is very similar to the other populations which have previously been investigated.

Pollock.—The diet of pollock was equally divided between fish and crustaceans (Table 1). Atlantic herring was the major species of fish preyed upon while the euphausiid, *Meganyctiphanes norvegica*, was the single most important prey. The significance of euphausiids in the diet of pollock had previously been noted by Kendall (1898) who found that *Thysanopoda* were virtually the exclusive prey for pollock taken off Eastport, Maine. Bigelow and Schroeder (1953) included Kendall's observations in their treatise on fishes in the Gulf of Maine but also mentioned that young herring were an equally important prey. Steele (1963) and Dexter (1969) again confirmed the importance of euphausiids such as *M. norvegica* as major prey for pollock in the Gulf of Maine.

However, Steele also remarked that fish were eaten in addition to euphausiids by the larger (75+ cm) pollock. The mean predator fork length for pollock taken in the Gulf of Maine (Table 3) during the present study (66.4 cm) was greater than for the fish caught on either Georges Bank (38.2 cm) or in Western Nova Scotia (44.6 cm). Accordingly, fish, especially Atlantic herring, were much more important as prey for the Gulf of Maine pollock than in either of the other two areas. In European waters the food of pollock appears to be similar to that of their American counterparts as they have also been reported to prey heavily on euphausiids (Wagner 1959; Mironova 1961; and see Nagabhushanam 1965 for a brief review in tabular form).

Silver hake.—Fish accounted for almost three-fourths of the diet of silver hake, with crustaceans making up the remaining prey (Table 1). Fish had previously been recognized as the major prey of the silver hake by Bigelow and Schroeder (1953). They described these predators as preying on herring or most any other smaller schooling fish or even the young of almost any of the fish commonly found in the Gulf of Maine. For example, Nichols and Breder (1927) found 75 herring, 7.62 cm long, in the stomach of a 59 cm silver hake. Bigelow and Schroeder (1953) also noted that silver hake ate squid if available while smaller hake fed on the shrimp *Pandalus*. Jensen and Fritz (1960) reported on the diet of silver hake collected in the northwest Atlantic. Expressing their data as the frequency of occurrence of prey, they also found that fish predominated in the stomachs of the larger silver hake while crustaceans, mostly euphausiids, were more common in the stomachs of the smaller fish. More recently, Vinogradov (1972) examined a total of 42,515 silver hake stomachs collected from fish caught in the northwest Atlantic. He also found that the smaller hake preyed on crustaceans, especially euphausiids, with a shift to fish as the major prey for hake >40 cm FL. Interestingly, all of these authors have commented on the cannibalistic nature of silver hake which was again recognized in this report, especially for fish taken in the Middle Atlantic (Table 4).

White hake.—The white hake and red hake resemble each other closely and the landings of these hakes have only been reported separately since 1944. Therefore, studies on the food habits of white hake alone are relatively rare. Linton (1901) examined the stomachs of some white hake but they were empty, and Hansen (1915) found some euphausiids, *Thysanoessa inermis,* in the stomachs he examined. Bigelow and Schroeder (1953) consider the food of the two hakes together although they specifically mention the occurrence of squid, crabs, butterfish, mackerel, and flounder in the stomachs of small white hake. Apart from the data given here (Table 1), which identifies white hake as being primarily piscivorous, the only other recent reports discussing the food of this fish are by Tyler (1971, 1972) and Petrov (1973). Tyler (1971) observed seasonal changes in the distribution and the diet of fishes in Passamaquoddy Bay, New Brunswick, Canada. White hake were present in the bay during summer and autumn. For the smaller white hake (total length range 15-26 cm) Tyler identified mysids, amphipods, and euphausiids as principal prey while the larger fish (28-45 cm) preyed upon shrimp, euphausiids, and fish. The data reported here are generally for larger fish (average total = 46.4 cm FL, see Table 1) than those considered by Tyler and this may explain our observation that white hake are primarily piscivorous. Petrov (1973) collected food habits data for the years 1969, 1971, and 1972 in ICNAF (International Commission for the Northwest Atlantic Fisheries) Subarea 3 which is north of our study area, off the eastern coast of Canada. Petrov's data are based on a subsample of the entire population and, although based on frequency of occurrence, show very similar results to those reported here (Table 1). He found that fish predominated in the diet with crustaceans being of secondary importance.

Offshore hake.—Biological data on the offshore hake is rare, and information on its food has only just become available. Rohr and Gutherz (1977) described the offshore hake as an active predator, preying on crustaceans and fish including other offshore hake. Juveniles were found to prey heavily on shrimp while maturing adults fed on fish, shrimp, and squid. The primary prey of adults was fish, but they also preyed upon caridean shrimp and squid. The offshore hake examined during the course of the present study confirm the observations of Rohr and Gutherz. The hake we examined preyed heavily on fish but also consumed crustaceans (i.e., caridean shrimp and euphausiids) and squid (Table 1).

Cusk.—Cusk were identified as being primarily fish-eaters, although crustaceans and echinoderms were also important prey, but to a lesser extent (Table 1). The cusk's piscivorous habits may be accounted for because of its heavy reliance on fish as prey in Western Nova Scotia (Table 7). In contrast, crustaceans made up 90% of the diet in the Gulf of Maine (Table 7), but because of the total weight of fish prey when all five geographic areas are combined, crustaceans are of secondary importance (Table 1). Little comparative data exist on the food of this animal, but it has been reported that crabs and occasionally molluscs were found in the stomachs of several cusk caught on Platt's Bank in the Gulf of Maine in 1924 (Bigelow and Schroeder 1953). Leim and Scott (1966) also noted that the cusk eat crabs and molluscs together with an occasional starfish. Our data confirm these observations but add fish as an important potential prey. Bigelow and Schroeder (1953) mention that the cusk is not fastidious as to the bait it will accept, taking clams, cockles, and herring quite readily. The diversity in the prey for the different geographic areas (Table 7) tends to corroborate their observations, that is, the cusk will prey on whatever animals are available.

Red hake.—The dietary information summarized by Bigelow and Schroeder (1953) is generally for both red and white hake combined although they do mention one

instance where the bellies of red hake were distended with sand lance, *Ammodytes* sp. In an earlier paper, Linton (1901) reported finding shrimp, amphipods, and the lenses of some small fish in red hake stomachs, and Breder (1922) noted that the one stomach he examined was full of prawns. From the current study (Table 1), red hake has been identified as a mixed feeder, preying on both fish and invertebrates. Crustaceans were the most important prey, followed by fish, molluscs, polychaetes, and echinoderms, in decreasing quantities. Vinogradov (1972) examined the stomachs of 5,486 red hake collected in the northwest Atlantic and, based on frequency of occurrence, found that invertebrates were the most important prey although substantial numbers of fish and squid were also consumed. Vinogradov's study was conducted from 1965 through 1967, and our study from 1969 through 1972. Over these years the major prey of northwest Atlantic red hake appears to have been the same, with any differences observed in the species composition of the diet most likely relating to differences in the sampling sites and local abundance of certain prey.

Spotted hake.—Spotted hake were identified as mixed feeders, relying on both crustaceans and fish as major prey (Table 1), although cephalopods were also somewhat important. Comparative data on the diet of these predators are scanty. Hildebrand and Schroeder (1928) noted mysids in the stomachs of small hake from Chesapeake Bay and Bigelow and Schroeder (1953) only mentioned the food of spotted hake in passing, noting that it fed on fish, squid, and crustaceans. More recently, Sikora et al. (1972) examined the gut contents of 341 juvenile spotted hake and identified crustaceans, especially the macruran mud shrimp, *Upogebia affinis,* as the most important prey, while fish ranked second in the diet. Comparative information on the food of adult spotted hake is completely lacking.

Haddock.—Haddock has a long history of commercial importance and as a result a voluminous amount of dietary information has been collected over the years and the literature on the North American stocks alone is reasonably extensive: Atwood 1866; Verrill 1871, 1873; Baird 1889; Willis 1890; Kendall 1898; Clapp 1912; Needler 1929; Vladykov 1933; Homans and Needler 1944; Bigelow and Schroeder 1953; Wigley 1956; Templeman 1965; Wigley and Theroux 1965; Kohler and Fitzgerald 1969; Tyler 1972.

In one of the earliest papers, Baird (1889) remarked that a complete listing of the prey of haddock would include almost all the fauna of any given area. An examination of the papers listed above gives much credibility to such a statement. It would be impossible to generally classify the haddock's dietary preferences except to say that they usually prey more heavily on benthic invertebrates than fish although they are highly opportunistic and will prey on, for example, fish eggs if they are available. Within one of the geographic areas considered here the diversity in the haddock's diet has been clearly demonstrated by Wigley (1956). He investigated the haddock's food habits on Georges Bank and found that the data warranted a division of the bank into three different food-type areas.

The results from our study (Table 1) indicate that ophiuroids were the most important prey and that polychaetes, crustaceans, and fish eggs ranked second in importance. The significance of fish eggs in the diet is of some interest. Bigelow and Schroeder (1953) stated that haddock have been accused of feeding on herring spawn but they doubted that this was true. Our observations do, in fact, confirm that haddock will prey greedily on herring spawn as had also been reported by Bowman (1923) and Nikolsky (1963). This type of feeding behavior is not uncommon since haddock have also been found to consume quantities of fish eggs when the capelin, *Mallotus villosus*, spawn in the Barents Sea (Tseeb 1960) and on the Grand Banks of Newfoundland (Templeman 1965). These results confirm the benthic nature of haddock feeding.

Fourbeard rockling.—According to Bigelow and Schroeder (1953) the food habits of the fourbeard rockling have not been investigated on this side of the Atlantic. From reports on the stomach contents of British and Scandinavian fish they concluded that the American fourbeard rockling would probably eat shrimp, isopods, other small crustaceans, and fish fry. Leim and Scott (1966) commented that much of the biology of the fourbeard rockling is unknown since it is rarely caught in commercial trawls because of its small size. They also suggested that it would eat small crustaceans and fish but gave no further details. In the study reported here, a total of 48 stomachs was examined and our observations confirm the suppositions of these previous authors. The major prey were found to be crustaceans, with the sand shrimp, *Crangon septemspinosa*, being of primary importance (Table 1).

Macrouridae.—There is little information on the food of either the marlin-spike or the longnose grenadier; however, other grenadiers are generalists in their feeding habits (Pearcy and Ambler 1974; Haedrich and Henderson 1974). We found that crustaceans and polychaetes were the major prey of the marlin-spike (Table 1). While too few fish were collected to make any firm conclusions regarding the feeding habits, our results agree with observations by Hansen (1915) and Bigelow and Schroeder (1953).

Ocean pout.—Ocean pout are a bottom fish which prey heavily on echinoderms and crustaceans (Table 1). Almost three-fourths of their diet consisted of the sand dollar while rock crabs and amphipods accounted for the majority of the crustaceans. Olsen and Merriman (1946) collected ocean pout in the southwestern part of the Gulf of Maine and in Southern New England where they identified the sand dollar as the major prey. They reported rock crabs and the amphipod, *Unciola*, as being of secondary importance although some fish had also eaten bivalve molluscs such as *Yoldia* and *Pecten*. Smith (1950)

examined the stomach contents of ocean pout collected in Block Island Sound, in Southern New England. The primary prey in this area was the amphipod, *Leptocherius pinguis,* with the sand dollar being the second most important prey. Tunicates were also important, making up almost 10% of the diet by weight. In the present study tunicates were again found to be a reasonably significant prey item but only in the Gulf of Maine. Bigelow and Schroeder (1953) examined the stomachs of ocean pout taken in Massachusetts Bay in 1924 and near the Nantucket Lightship in 1950. They found that the rather large specimen from Massachusetts Bay was full of brittle stars and spider crabs while the animals taken near the Lightship were full of small sea scallops.

Dietary Overlap

The percentage similarity in diet (Fig. 3 and text) is a relative measure of overlap of the food habits, where overlap is simply defined as the use of the same resource by more than one predator regardless of the resource abundance. In contrast, resource competition exists only if the demand for prey outstrips the immediate supply (Weatherley 1963; Keast 1965, 1977; Zaret and Rand 1971). The index of diet overlap presented here, therefore, just highlights the potential for food resource competition between these fish populations which could exist if certain prerequisites were met, as discussed below.

The distribution of many of these fish, especially the commercially important species, has been documented from the groundfish survey data collected by the personnel at the Woods Hole Laboratory (Colton 1955, 1972; Fritz 1965; Grosslein and Bowman 1973; Grosslein and Clark 1976[3]). The ranges of many of these predators overlap, however, the major concentrations of the different species of fish are not usually the same. Fritz (1965), for example, has summarized the distribution of seven gadids from the autumn groundfish survey data, 1955-61. His results showed that silver hake were ubiquitous, but over the 6-yr study they were most abundant off Cape Cod and to the south, and also on the western and southeastern parts of Georges Bank. Atlantic cod occurred north of lat. 41°00′ and were abundant off Nantucket, north of Cape Cod, and southeast of Nova Scotia. The haddock, pollock, and white hake might be considered boreal species as they, like the Atlantic cod, all occurred north of lat. 41°00′. The major concentration of haddock was on the northern edge of Georges Bank and on Browns Bank. Pollock were abundant near Nova Scotia but also occurred in moderate concentrations in the Gulf of Maine. White hake were found along the northeastern edge of Georges Bank and also in the Gulf of Maine. Red hake occurred throughout the area ranging from Nova Scotia to Cape May, N.J., being most abundant south of Cape Cod. A more recent summary of the groundfish survey data has been prepared by Grosslein and Clark (see footnote 3). This document includes both spring and autumn cruise data which gives some idea of the seasonal changes in the distribution of the commercially important gadoids. Although certain species, such as red hake, have distinct seasonal migrations, the overall distribution of many of these fish is reasonably constant throughout the year and even from year to year. Colton (1972), for example, found no major change in the general distribution of the haddock during the period 1950-68 despite changing trends in seawater temperature. From this survey data it may tentatively be concluded that, on a broad scale, although some spatial overlap occurs between many of the 15 gadiform fishes we have studied, the major concentrations of each fish are usually sufficiently distinct so that competition between the various populations for the same food resource would be minimal. On a more localized scale, however, spatial overlap may occasionally be severe as has been documented by Grosslein and Bowman (1973). They considered the problem of bycatch in ICNAF Subareas 5 and 6 (Georges Bank to Cape Hatteras), pointing out that a bottom trawl fishery in these areas could not be conducted without harvesting a substantial mixture of species. In particular, aggregates of red and silver hake are consistently found in Southern New England as are mixtures of Atlantic cod, haddock, and hake on Georges Bank. For situations such as these, food habits studies would have to be conducted on fish collected from mixed catches to determine if the fish are feeding on the same prey at the same time or if there is significant resource partitioning, thus eliminating the potential for competition as was found by Jones (1978) for some gadoid fishes in European waters.

Even if spatial overlap were to occur on a significant scale, it may further be counteracted by short-term temporal changes in predator distribution and activity. Daily activity cycles may effectively function to segregate predators although the predators would, at times, share the same prey (Graham 1924; Rae 1967; Brunel 1972; Daan 1973; Arntz 1974; Jenkins and Green 1977).

Finally, even when the spatial and temporal distribution of these species is accounted for, it is difficult to make firm conclusions regarding resource limitation without an extensive knowledge of the benthic community available for exploitation. Studies such as those conducted by Arntz (1971, 1973, 1974) which combine food habits investigations, feeding chronology experiments, and a quantitative evaluation of the macrobenthos are needed before we can quantitatively determine the degree to which food resource competition actually exists.

A number of nonbiological factors may also influence the calculation of dietary overlap and these must be accounted for when interpreting overlap data. The level of identification of the prey will affect the overlap calculations since broader taxonomic groupings actually increase the observed degree of overlap. Moyle (1977) gave an example of this when comparing the diet of sculpins

[3]Grosslein, M. D., and S. H. Clark. 1976. Distribution of selected fish species and status of major fisheries in the Northwest Atlantic. Technical reference document for bilateral negotiations between USA and Canada. NOAA, NMFS, Northeast Fisheries Center Lab. Ref. 76-12, 171 p.

and some salmonids, noting that the greatest overlap occurred when the prey was only identified to the order level. In the present study the same effect may be observed. If, for example, the percentage similarity is calculated for the diet of Atlantic cod and silver hake at the highest taxonomic level given in Table 2, the similarity increases from 58% (Fig. 3) to 89%. On the other hand, Keast (1977) justified the use of broader taxonomic groupings for sorting prey; he argued that the body size of the prey rather than finer taxonomic identity is important for studies on fish food habits. It would appear that there exists an optimal level of taxonomic classification for prey identified for dietary overlap calculations. This optimum is probably primarily dependent on the size of the prey, provided the prey shares a similar ecological niche, since size dependent prey selection has been well-documented for fish (Keast 1965; Tyler 1972; Daan 1973; see also Edwards 1976). Apart from the level of taxonomic identification, sample size is probably the second most important nonbiological factor influencing dietary overlap calculations. The smaller the sample the more variable the percentage similarity. This effect was noted in the results for the marlin-spike and longnose grenadier where a relatively small change in sample size, and, consequently, in the quantity of prey consumed, could have a large influence on the observed composition of the diet and any resulting overlap estimates.

Bearing in mind some of the limitations discussed above, an overall pattern emerges from calculating and categorizing the percentage similarity between the fishes' diets (Fig. 3) which is not as readily apparent from a cursory examination of the tables on stomach contents for each of the 15 predators alone. Generally, the greatest block of similarity occurs in the upper left section of Figure 3 while the lowest level of overlap is in the upper right-hand section of the same figure. This reflects two distinct feeding types as revealed by an examination of the data in Table 2. Thus, fish populations such as Atlantic cod, pollock, silver hake, white hake, offshore hake, and cusk are decidedly piscivorous while the haddock, longfin hake, fourbeard rockling, marlin-spike, longnose grenadier, fawn cusk-eel, and ocean pout are characterized more as benthic, invertebrate feeders. Red and spotted hake are intermediate, resulting in a very similar diet which overlaps both the piscivores and benthic invertebrate feeders.

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