

International Commission for



the Northwest Atlantic Fisheries

Serial No. 3681  
(D.c.5)

ICNAF Res.Doc. 75/IX/130<sup>1</sup>

SEVENTH SPECIAL COMMISSION MEETING - SEPTEMBER 1975

A preliminary description of some  
important feeding relationships

by

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Abstract

Quantitative data from the analysis of 28 species of fish, approximately 18,500 stomachs collected from Cape Hatteras to Western Nova Scotia during 1969-72 are arranged to show trophic relationships among selected consumer groups. Seven groups are identified as invertebrate feeders while three are identified as fish feeders. The food content of each group is related to the nature of its diet.

The major foods of cod, *Gadus morhua* (Linnaeus); haddock, *Melanogrammus aeglefinus* (Linnaeus); and silver hake, *Merluccius bilinearis* (Mitchill) are presented. Only a slight regional variation in dominance among the major food groups was detected.

Squid is shown to be a significant component of the diet of some demersal fish with 48 predators, pelagic and demersal, being identified.

Competition between herring, *Clupea harengus harengus* Linnaeus and mackerel, *Scomber scombrus* Linnaeus was measured using an overlap index. Results indicate that herring and mackerel are feeding on the same types of organisms, however, in substantially different proportions.

Introduction

The overall trophic economy of an ecosystem depends on how the food resource is divided among the consumer components (Steele, 1974).

The purpose of this document is to indicate the inter-specific trophic relations among selected consumer groups by analysis of their food habits. This report is divided into 4 parts:

- 1) presentation of a multispecies predator-prey matrix, highlighting trophic interactions among 28 predator species;
- 2) a closer look at 3 major predators; cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and silver hake (*Merluccius bilinearis*), with a consideration of regional food habits;

<sup>1</sup> All ICNAF documents will now be numbered to include the month (in Roman numerals) of the meeting at which they were presented.

- 3) review of squid predators and relative importance of squid in the diets of some North Atlantic fish; and
- 4) a brief analysis of inter-specific competition between herring and mackerel.

#### Source of data

Some 80 species of fish were collected by the Northeast Fisheries Center, Woods Hole, from Cape Hatteras to the Nova Scotian shelf (Figure 1), during 9 standard groundfish surveys, 1969 to 1972 (Table 1). Specimens were selected at random from the survey catches for food studies. For the present analysis, 28 species were selected (with sufficient sampling heterogeneity to minimize seasonal and regional bias) and grouped according to Table 2. The data presented represents the quantitative analysis (wet weight in grams) of the stomach contents of approximately 18,500 adult specimens.

#### Data analysis

The food habits information for each predator species represents a collation of data over all areas and all seasons sampled. So that interactions could be assessed on an equal basis the prey weight in grams was pro-rated to a metric ton of predator (see Table 3). Thus, for example, a metric ton of cod would have consumed 66 grams of haddock, 414 g redfish, 305 g yellowtail, etc.

Squid represent only the commercial species *Loligo* and, or *Illex*. The deep water forms such as *Rossia* have been omitted.

The terms predator and prey are used to denote the consumer (predator) and the items which are consumed (prey), and does not necessarily imply active pursuit or hunting on the part of the consumer.

The values in Table 3 are underestimates of the quantity consumed in all prey categories due to the inclusion of an excess number of empty stomachs in the calculations. This arises from the difficulty in determining whether a stomach is naturally empty or is empty due to induced regurgitation.

The prey category "other finfish" includes the weight of unidentified fish, fish eggs, and those which could only be identified to a higher taxa (e.g. gadidae), resulting in an overestimate for "other finfish" and a further underestimate for the other fish categories.

#### A multispecies predator-prey matrix

The results of the analysis of the multispecies assemblage are presented in Table 3. If the diet of the 28 species are considered collectively, total column far right, fish (eaten by 25 species) constituted 46% of the diet while invertebrates (eaten by all 28 species) slightly dominated at 54%, including 2.1% squid. Of the specific predator categories the major piscivorous species were silver hake, 72%; cod, 69%; and the other finfish category, 63%. The diets of all other species were strongly dominated by invertebrates; haddock, 98%; redfish, 98%; yellowtail, 99%; herring 99%; mackerel, 95%; other flatfish, 94% and pollock, 69%.

The potential for interaction between species can be more easily seen by considering the distribution of each prey item among the predators.

Cod - No predators were identified for cod. Indeed, adult cod were larger and more active than most other groundfish considered in this report. The diets of the larger natural predators such as sharks, porpoise and whales are not known from the study area. However, small cod (5-20 cm) were probably eaten in substantial quantities by other groundfish but due to the difficulty in separating small cod, haddock and pollock, especially those in a semi-digested state, smaller cod become lumped with other small gadids at the family level (Gadidae) and therefore were included in the "other finfish" category.

Haddock - Predators include cod, pollock and other finfish. Haddock, a minor prey item, accounted for only 0.5% of all fish consumed (right hand column). It should be noted, however, that the density of haddock was

- Redfish - Cod, haddock, and other finfish were redfish predators. Redfish comprised about 3.5% of the total fish eaten by all predators considered.
- Yellowtail - This flatfish constituted 2.5% of the fish component of the cod diet. Yellowtail was relatively insignificant as a prey item for silver hake and other finfish, and contributed only 1.1% of all fish eaten.
- Other flatfish - Other flatfish were of about equal but minor importance in the diets of cod and other finfish and make up only 1.5% of the fish component of the total predator column.
- Herring - Herring constituted a major portion of the diets of cod (15%) and silver hake (10%). Pollock and other finfish were insignificant predators. Herring accounted for 11% of the fish eaten by all predator species combined.
- Mackerel - Mackerel, like herring was a significant component, constituting 19% of the silver hake diet and 15.2% of the other finfish (primarily spiny dogfish) category. Cod was a minor predator with only 2.7% of its diet weight being mackerel.
- Pollock - No significant predators were identified for pollock presumably for the same reasons presented for cod earlier. Cannibalism, larger pollock eating smaller pollock, was indicated but insignificant, comprising only 0.1% of the pollock diet.
- Silver hake - Six predator categories were identified for silver hake. It accounted for 4.7% of the flatfish diet, 2.1% of the mackerel diet, 1.4% of the pollock diet, 2.3% of the other finfish diet, and a small amount in the cod diet. Cannibalism, 3.5% was more significant in the silver hake diet than any other species considered.
- Other finfish - This category shows the relative importance of fish in the diet of the predator species. Again it is quite easy to identify the more piscivorous groups, cod, pollock, silver hake and other finfish. An expansion of this section of the matrix is needed before many specific predator-prey interactions can be identified.
- Squid - Squid were found in the diet of 4 categories: other flatfish, 4% (diet weight), silver hake, 2%, other finfish (bluefish, spiny dogfish and goosfish), 8.4% and present in a minor quantity in the mackerel diet.
- Other invertebrates - These values illustrate the significance of the invertebrates as a food source for most marine fish. Again, invertebrate prey was dominant in the diets of 18 of the 28 species analyzed, constituting 52.2% of all prey consumed by the 28 species considered.
- Invertebrate components of haddock, yellowtail, other flatfish, herring and mackerel were all between 2,000 and 3,000 grams. Two other predators, cod and redfish, consumed between 3,400 and 5,400 grams while the invertebrate component for pollock was extremely high, 10,490 grams.

#### Relative importance of prey groups

The importance of each prey category to the multispecies assemblage can be determined by comparing the totals which appear in the far right hand column. Other finfish, mackerel, herring, and silver hake were major contributors to the fish component of the prey biomass. Squid accounted for 2.1% and other invertebrates for 52.2% of the total prey biomass consumed by the 28 predator species.

#### A static comparison of food intake

The bottom row of figures in Table 3 gives the relative consumption or food intake in grams per metric ton of predator if it were measured at a single point in time hence, static food intake. Figure 2 presents the same information in bar graph form.

Cod contained more prey than any other predator, some 22% of the prey biomass total (78,073 g). Two other gadids, pollock and silver hake, and other finfish contained 20%, 17%, and 18%, respectively.

The six remaining groups shared the residual 23% as follows: redfish, 6%, haddock, 4%, herring, 4%, other flatfish, 4%, yellowtail, 3%, and mackerel, 3%.

The food content is related to the percent fish in the diet (Figure 2). Generalizing, those predators with a high percentage of fish in their diets (fish feeders) have a high food content and those with an extremely low percentage of fish in their diets (invertebrate feeders) have a correspondingly low food content. Some 77% of the total prey biomass was proportioned among the fish feeders while 23% was distributed among the invertebrate feeders.

For a better understanding of Figure 2 such things as digestive efficiency, time of digestion, feeding rate, feeding chronology, and individual feeding behavior of each predator must be known.

#### Special consideration of three major gadid species

Bowman<sup>1/</sup> (1975), has recently analyzed the food habits of cod, silver hake, and haddock utilizing the same data base (1969-1972) as is presented in the multispecies analysis. This section summarizes some of Bowman's results as regards the general and regional food habits of those species.

According to Clark and Brown (1975), five species, cod, haddock, silver hake, red hake, and pollock account for approximately 67% of the biomass of all demersal fish. Of this, cod, silver hake, and haddock comprise 76% of the total gadid biomass. Therefore it is imperative that we understand the division of available resources among these three major gadid species.

In general silver hake and cod are better described as "mixed feeders" although their diets are both predominantly fish. The silver hake stomach contents consist of 96% fish and crustaceans, while the cod diet is 80% fish and crustaceans. A diverse invertebrate fauna characterizes the haddock diet, which consists of 35% echinoderms and lesser amounts of crustaceans and polychaetes.

Only silver hake were sampled in sufficient numbers from the Middle Atlantic and Southern New England to be considered in those regions. The food habits of all three species will be presented for Georges Bank, the Gulf of Maine, and Western Nova Scotia.

Middle Atlantic. The silver hake diet consisted chiefly of fish, other silver hake, and lanternfish (myctophids). Crustaceans, primarily krill shrimp (euphausiids), sand shrimp (*Crangon*), and the deepwater shrimp (*Dissalopandalus*), were of secondary importance.

Southern New England. Fish again dominated silver hake diet with mackerel (Scombridae) being most common followed by other gadids and butterfish. Cannibalism was the highest in this area, 7% of the diet weight.

Georges Bank. Cod fed primarily on sculpin eggs, 14% diet weight and other fish, 12% diet weight, including yellowtail, sculpins, and gadids.

While 80% of the silver hake diet consisted of fish, only lanternfish (myctophids) and silver hake were identifiable.

<sup>1/</sup> R. Bowman. Food habits of cod, silver hake, and haddock from the Northwest Atlantic, 1969-1972. Northeast Fisheries Center, Lab. ref. 75-1.

Polychaetes (24%) and crustaceans (23%) were the chief food items of haddock. The polychaete component consisted of terebellid, sabellid, and nereid forms and the crustacean component of gammarid amphipods and krill shrimp (*Meganyotiphanes*).

Gulf of Maine. Fish again dominated the cod diet which consisted of 27% herring with lesser amounts of redfish, mackerel, and gadids. Crustaceans accounted for 23% of the cod diet, primarily the deep-sea red crab (*Geryon*).

The silver hake were also feeding heavily on herring, 28% diet weight, which was followed in importance by mackerel (scombridae) and alewives. Crustaceans, a minor element of the silver hake diet, included krill shrimp (*Meganyotiphanes*), glass shrimp (*Pasiphaea*), and deepwater shrimp (Pandalidae).

Echinoderms dominated the haddock diet (53%), composed primarily of brittle stars (*Ophiura*), sea urchins (Echinoidea), and sea cucumbers (*Thyone*).

Western Nova Scotia. The cod diet consisted mainly of fish, sand lance (12%), herring, and gadids. Crustaceans consumed include krill shrimp (*Meganyotiphanes*), toad crabs (*Hyaas*), and pandalid shrimp.

The silver hake diet was dominated by two items; gadid fish account for over 50% of the diet and krill shrimp (*Meganyotiphanes*) constitute an additional 28%.

In contrast, echinoderms again dominate the haddock diet, primarily brittle stars (*Ophiopholis* and *Ophiura*), sea urchins (*Strongylocentrotus*), and sea cucumbers (*Psolus*).

#### Predator-prey relationships of squid (*Loligo* and *Illex*)

Literature review. A brief review of the literature identifies 48 predators of squid, listed in Table 4, which includes many demersal as well as pelagic species. The pelagic group contains a contingent of large fast moving predators, swordfish, the bluefin tuna, skipjack tuna, and seven sharks. The smaller sharks are the sand tiger, porbeagle, night shark, smooth dogfish, and the spiny dogfish. Two larger oceanic species, the thresher and white sharks, are also listed.

The largest squid predator, specifically reported from the ICNAF area by Mercer (1974) is the northern pilot whale.

The smaller pelagic species include; the alewife, john dory, croaker, silverside, bluefish, butterfish, hickory shad, scup, and weakfish.

Some 22 species of demersal fish are also reported as squid predators; gadids, flatfish, skates, goosefish, sea raven, sea robin, redfish, grenadier, and tilefish.

The list which appears in Table 4 is not complete, but it does identify most major predators of adult squid in the ICNAF area.

#### Relative importance in fish diets.

Of the 28 species analyzed for this report eleven were identified as squid predators. The relative importance of squid in the diets of these eleven fish are shown in Table 5.

Only two pelagic predators are listed. Bluefish ranks as the most important predator, as squid constitute 30.5% of the diet weight. This fish is known for its voracious feeding habits and has been observed "tearing" through large schools of squid (Bigelow and Schroeder, 1953). Although mackerel seem to possess the speed and size necessary to be a successful squid predator, squid represents only 0.1% of the diet weight.

The high percentage of squid in the stomach contents of the nine remaining demersal species is quite surprising. Some higher percentages include sea raven, 19.9%; fourspot flounder, 17.7%; spiny dogfish, 12.6%; and goosefish, 12.2%. Squid are less important in the diets of the other demersal fish such as silver hake, 2.1% and white hake, 1.8%.

Interaction with the demersal community may be associated with observed squid behavior. Observers aboard research submersibles have reported that squid frequently lie in a "resting position" on the bottom. During this period individuals appear to be quite lethargic and therefore subject to substantial predation by demersal predators.

#### Herring and mackerel competition study

A special food and feeding study was undertaken in the Spring of 1974. The aim of these studies was to identify the major food items of herring and mackerel and to attempt to analyze the degree of inter-specific competition with regard to feeding. Analysis was carried out on the basis of wet weight of each food organism present. Preliminary results show that herring fed mainly on chaetognaths (43%) and euphausiids (34%) and pteropods (6.2%) and mackerel fed mainly on calanoid copepods (32.7%) and pteropods (33.5%).

A comparison of genera from the stomachs of each species, Table 6, shows that 16 of the 29 food items identified were shared by both species. The extent of diet overlap (Horn, 1966) was measured, based on quantitative stomach analyses. Results indicated that there was considerable diet overlap (0.82) when calculated for frequency of occurrence, however, only a small amount of overlap (0.12) when based on percent stomach content weight. Therefore a general conclusion would be that herring and mackerel are eating the same kinds of organisms, however, in substantially different proportions.

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Table 1. Distribution of stomach samples collected by NEFC, Woods Hole, between 1969 and 1972.

CRUISE	YEAR	SEASON	NO. SPECIES	NO. FISH
69-11	1969	Fall	27	1637
70-6	1970	Fall	22	2672
71-1	1971	Spring	31	3298
71-4	1971	Fall	5	78
71-6	1971	Fall	26	1406
72-1	1972	Winter	16	471
72-2	1972	Spring	43	3715
72-5	1972	Summer	3	12
72-8	1972	Fall	37	3063

Table 2. Species categories considered in the matrix analysis. The number of fish analyzed appears in parentheses.

ICNAF MANAGEMENT SPECIES	OTHER FLATFISH	OTHER FINFISH
1. Cod (1706)	1. Fourspot flounder (895)	1. Alewife (136)
2. Haddock (1369)	2. Sand flounder (120)	2. Scup (346)
3. Redfish (921)	3. Witch flounder (955)	3. Butterfish (452)
4. Yellowtail (2715)	4. American plaice (988)	4. Bluefish (46)
5. Herring (344)	5. Winter flounder (115)	5. Spotted hake (333)
6. Mackerel (278)		6. White hake (610)
7. Pollock (587)		7. Red hake (933)
8. Silver hake (2330)		8. Ocean pout (238)
		9. Goosefish (250)
		10. Wolffish (176)
		11. Sea raven (108)
		12. Longhorn sculpin (908)
		13. Spiny dogfish (382)
		14. Little skate (393)
		15. Smooth skate (87)

Table 3. Predator-prey relationships expressed as grams prey per metric ton predator.

PREY	PREDATORS											TOTAL
	COD	HADDOCK	REDFISH	YELLOWTAIL	OTHER FLATFISH	HERRING	MACKEREL	POLLOCK	S. HAKE	OTHER FINFISH	TOTAL	
COD	-	-	-	-	-	-	-	-	-	-	-	-
HADDOCK	66	-	-	-	-	-	-	38	-	78	182	
REDFISH	414	-	-	-	-	-	-	10	-	160	584	
YELLOWTAIL	305	-	-	-	-	-	-	-	7	94	406	
OTHER FLATFISH	280	-	-	-	-	-	-	-	-	259	539	
HERRING	2592	-	-	-	-	-	-	22	1317	18	3949	
MACKEREL	484	-	-	-	-	-	-	-	2406	1375	4265	
POLLOCK	-	-	-	-	-	-	-	5	-	-	5	
SILVER HAKE	115	-	-	-	153	-	50	222	322	337	1199	
OTHER FINFISH <sup>1</sup>	7631	73	73	18	59	22	69	4486	5520	6714	24556	
SQUID	-	-	-	-	124	-	17	-	266	1207	1614	
OTHER INVERTEBRATES	5399	2897	4578	2095	2869	2799	2238	10490	3415	3994	40774	
TOTAL	17486	2970	4651	2113	3196	2821	2374	15273	12953	14236	78073	

<sup>1</sup>This prey category includes other finfish (Table 2), unidentifiable fish of all species, and fish eggs.

Table 4. A list of squid predators and references.

PREDATOR	REFERENCE	PREDATOR	REFERENCE
1. Alewife	1/Arvidson, Manuscript Report	13. Butterfish	Bigelow and Schroeder, 1953
2. American John dory	Bigelow and Schroeder, 1953	14. Fourspot flounder	Bigelow and Schroeder, 1953 Maurer and Bowman, 1975 Arvidson, Manuscript Report
3. Atlantic angel shark	2/Maurer and Bowman, 1975	15. Goosefish	Schroeder, 1895 Field, 1907 Bigelow and Schroeder, 1953 Maurer and Bowman, 1975 Arvidson, Manuscript Report
4. Atlantic bonito	Bigelow and Schroeder, 1953	16. Haddock	Homans and Needler, 1944 Wigley, 1956 Wigley and Theroux, 1965 3/Bowman, 1975 Arvidson, Manuscript Report
5. Atlantic croaker	Maurer and Bowman, 1975	17. Hickory shad	Bigelow and Schroeder, 1953 Arvidson, Manuscript Report
6. Atlantic silverside	Bigelow and Schroeder, 1953 Mulkana, 1966	18. Little skate	Field, 1907 Bigelow and Schroeder, 1953 Richards <i>et al.</i> , 1963
7. Atlantic tomcod	Bigelow and Schroeder, 1953	19. Night shark	Maurer and Bowman, 1975
8. Bamdoor skate	Bigelow and Schroeder, 1953 Arvidson, Manuscript Report	20. Northern pilot whale	Mercer, 1974
9. Barrelfish	Bigelow and Schroeder, 1953		
10. Black sea bass	Bigelow and Schroeder, 1953		
11. Bluefin tuna	Crane, 1936 Bigelow and Schroeder, 1953 Dragovich, 1970		
12. Bluefish	Bigelow and Schroeder, 1953 Grant, 1962 Lux and Mahoney, 1972 Maurer and Bowman, 1975		

1/ Arvidson, Manuscript Report, Northeast Fisheries Center, Woods Hole  
 2/ Maurer, R. O. and R. Bowman. Food habits of some marine fish from the Northwest Atlantic. Northeast Fisheries Center, Lab. ref. 75-3.  
 3/ Bowman, R. Food habits of cod, silver hake and haddock from the Northwest Atlantic 1969-1972. Northeast Fisheries Center, Lab. ref. 75-1.

Table 4. cont'd

PREDATOR	REFERENCE	PREDATOR	REFERENCE
21. Northern searobin	Bigelow and Schroeder, 1953	31. Sand tiger	Bigelow and Schroeder, 1953
22. Offshore hake	Maurer and Bowman, 1975	32. Scup	Bigelow and Schroeder, 1953 Arvidson, Manuscript Report
23. Opah	Bigelow and Schroeder, 1953	33. Sea Raven	Maurer and Bowman, 1975
24. Oyster toadfish	Field, 1907 Gudger, 1910 Bigelow and Schroeder, 1953 Schwartz and Dutcher, 1963	34. Silver hake	Dexter, 1969 Vinogradov, 1972 Bowman, 1975
25. Porbeagle	Scattergood, 1949 Bigelow and Schroeder, 1953	35. Skipjack tuna	Bigelow and Schroeder, 1953
26. Rainbow smelt	Kendall, 1927 Bigelow and Schroeder, 1953	36. Smooth dogfish	Breder, 1921 Bigelow and Schroeder, 1953 Maurer and Bowman, 1975 Arvidson, Manuscript Report
27. Redfish	Bigelow and Schroeder, 1953 Kelly, 1961 Dexter, 1969 Konchins, 1970	37. Spiny dogfish	Bowers, 1906 Field, 1907 Bigelow and Schroeder, 1953 Jensen, 1966 Maurer and Bowman, 1975 Arvidson, Manuscript Report
28. Red hake	Bigelow and Schroeder, 1953 Vinogradov, 1972 Arvidson, Manuscript Report	38. Swordfish	Bigelow and Schroeder, 1953 McKenzie, 1959 Tibbo, et al., 1961 Scott and Tibbo, 1968
29. Roughtail stingray	Maurer and Bowman, 1975		
30. Roundnose grenadier	Podrazhanskaya, 1971		

Table 4. cont'd

PREDATOR	REFERENCE	PREDATOR	REFERENCE
39. Thorny skate	Maurer and Bowman, 1975	44. White hake	Maurer and Bowman, 1975
40. Threespine stickleback	Bigelow and Schroeder, 1953	45. White perch	Bigelow and Schroeder, 1953
41. Thresher shark	Bigelow and Schroeder, 1953	46. White shark	Bigelow and Schroeder, 1953
42. Tilefish	Bigelow and Schroeder, 1953 Arvidson, Manuscript Report	47. Winter skate	Bigelow and Schroeder, 1953 Arvidson, Manuscript Report
43. Weakfish	Bigelow and Schroeder, 1953 Maurer and Bowman, 1975	48. Witch flounder	Summer et al., 1913 Linton, 1921 Nichols and Breder, 1927 Smith, 1950 Maurer and Bowman, 1975

Table 5. The relative quantitative importance of squid in the generalized diets of some North Atlantic fish.

PREDATORS	PERCENT DIET WEIGHT
1. Bluefish	30.5
2. Sea raven	19.9
3. Fourspot flounder	17.7
4. Spiny dogfish	12.6
5. Goosefish	12.2
6. Witch flounder	2.8
7. Silver hake	2.1
8. White hake	1.8
9. Red hake	1.2
10. Offshore hake	0.9
11. Atlantic mackerel	0.1

Table 6. Co-occurring generic food items in herring and mackerel. (Present, +, Absent, -).

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

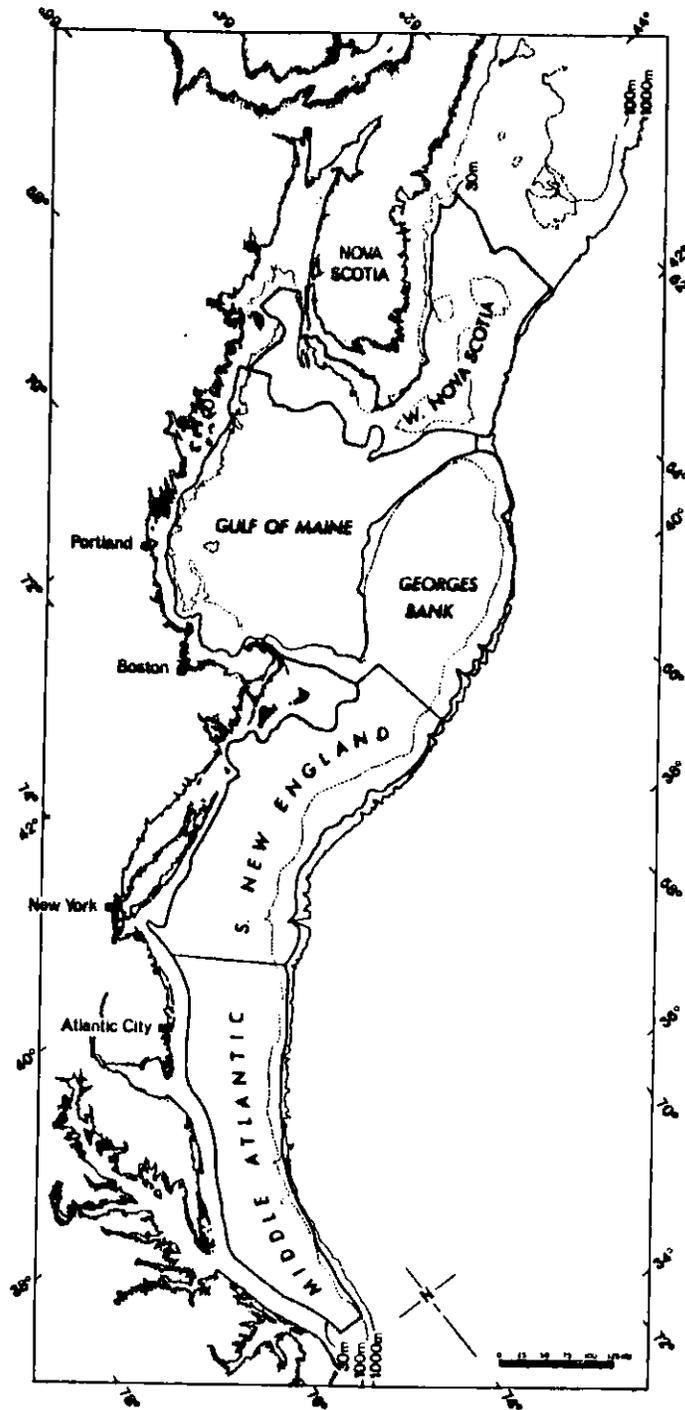


Fig. 1. Areas sampled from 1969 to 1972 by the Groundfish Survey Unit, NEFC, Woods Hole.

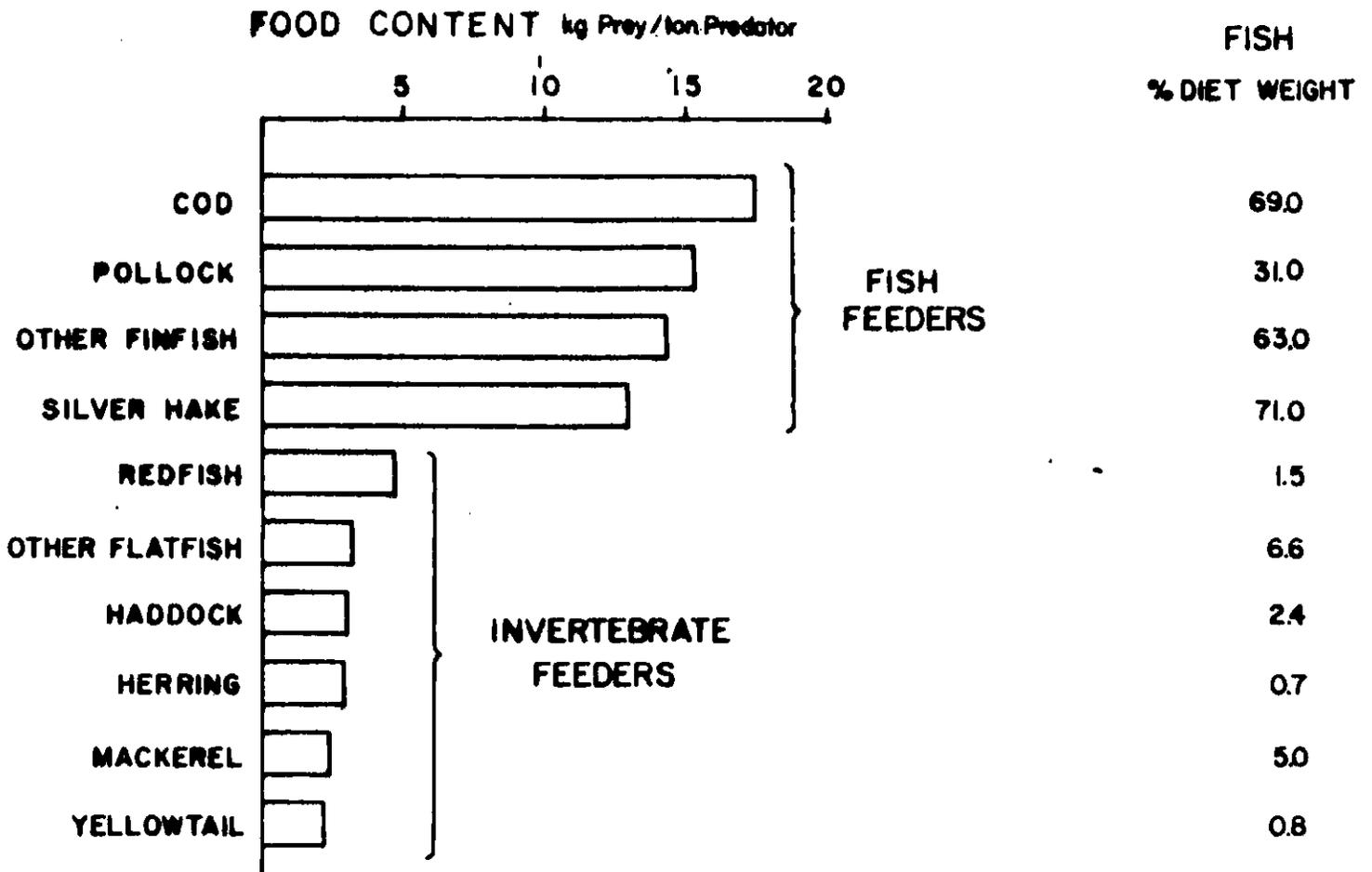


Figure 2. Relative food content of predator groups.