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Food of Silver Hake, Red Hake and Other Fishes of Georges Bank and Adjacent Waters, 1968-74*

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Abstract

Data on feeding of various pelagic, near-bottom and bottom fishes of Georges Bank and adjacent waters are examined. The species are grouped and discussed according to dietary similarities. Comparisons are made between the feeding spectra of silver hake, red hake, Atlantic herring, Atlantic mackerel, pollock, Atlantic cod, haddock, white hake, spiny dogfish, American angler, Atlantic sea raven, yellowtail flounder and American plaice. Although the feeding of silver hake and red hake is shown to be influenced by homologous ecological factors, production of these species depends on different ecological groups of food organisms, silver hake mainly on pelagic forms and red hake mainly on benthic forms. Silver hake was found to be one of the most significant predators of young silver hake and red hake in the ecosystem of the region.

Introduction

During the past two decades, the fish populations of the Northwest Atlantic have declined as a consequence of fishing pressure. Edwards (1976) considered that unregulated fishing was the main reason for the decline in catches of the major commercial fish species. Recently (1976-80), the fisheries were regulated by using maximum sustainable yields of the various species as guidelines for establishing total allowable catches. However, Edwards (1976) doubted that yield calculations alone were sufficient. The impacts of predators must also be taken into account, as well as the competitive relationships between fishes which are utilized as food by man (Edwards, 1976; Noskov and Vinogradov, 1977). Studies on the food and feeding of silver hake and red hake (important species of commercial interest on Georges Bank and in adjacent waters) and other species, such as Atlantic mackerel, Atlantic herring, spiny dogfish, yellowtail flounder, Atlantic cod and haddock, are needed to better understand the possibilities of increasing production and catches.

This paper summarizes feeding data which were collected during studies on the distribution and abundance of silver hake and red hake on Georges Bank and in adjacent waters. The results of this research are considered with data on fish feeding and abundance from many sources but concentrates on ichthyofauna of commercial interest (Bigelow and Schroeder, 1953; Jensen, 1966; Leim and Scott, 1966; Vialov and Karasiov, 1967; Rikhter and Vinogradov, 1969; Bailey *et al.*, 1970; Efanov and Vinogradov, 1973; Maurer, MS 1976; Jones and Geen, 1977; Rass, 1979).

Materials and Methods

Stomachs of silver hake, red hake and other fish species were collected during trawling operations of USSR research and exploratory vessels and during joint USSR-USA trawl surveys of Georges Bank and adjacent waters in 1968-74 (Fig. 1). The stomachs were taken from random fish samples of catches during 24-hr per day trawling and preserved for laboratory analysis. The contents of the stomachs were separated into identifiable components and weighed, and the food components were expressed as percentages of the total weight of the stomach contents for each species sampled.

Stomach contents of 26,542 fish specimens belonging to 27 species and 13 families were analyzed (Table 1). For quantitative assessment of the food relationships among the fishes, an index of food similarity (FS-coefficient), as suggested by Shorygin (1952), was used. For this, the percentage food composition of any two fish species was taken and the food organisms common to both were recorded. The sum of least percentages gives a food similarity index, irrespective of the occurrence of a given organism in the food composition of one or the other fish species.

Results and Discussion

Although bottom-trawl surveys are designed to estimate the distribution and abundance of groundfish species (i.e. fishes living on or near the bottom), the catches may also contain a variety of species which typically live pelagically. In the Georges Bank and

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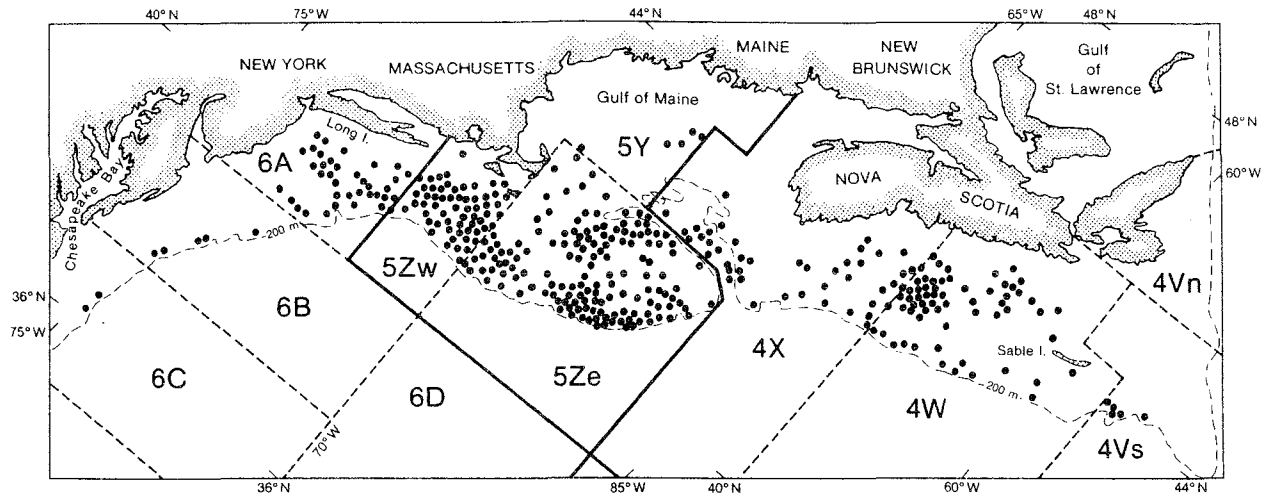

Fig. 1. Station locations and areas where fish stomachs were collected for the feeding studies, 1968–74.

TABLE 1. Numbers of stomachs of various fish species collected in Georges Bank and adjacent waters, 1968–74.

Family	Common name	Scientific name	No. of stomachs
Squalidae	Spiny dogfish	*Squalus acanthias* L.	815
Rajidae	Little skate	*Raja erinacea* Mitchill	253
	Winter skate	*Raja ocellata* Mitchill	52
	Thorny skate	*Raja radiata* Donovan	47
Clupeidae	Blueback herring	*Alosa aestivalis* (Mitchill)	431
	Alewife	*Alosa pseudoharengus* (Wilson)	835
	Atlantic herring	*Clupea harengus* L.	2,215
	Round herring	*Etrumeus sadina* (Mitchill)	176
Argentinidae	Atlantic argentine	*Argentina silus* Ascanius	174
Gadidae	Atlantic cod	*Gadus morhua* L.	537
	Haddock	*Melanogrammus aeglefinus* L.	811
	Silver hake	*Merluccius bilinearis* (Mitchill)	7,649
	Pollock	*Pollachius virens* (L.)	97
	Spotted hake	*Urophycis regius* (Walbaum)	35
	White hake	*Urophycis tenuis* (Mitchill)	88
	Red hake	*Urophycis chuss* (Walbaum)	3,848
Scombridae	Atlantic mackerel	*Scomber scombrus* L.	4,370
Zoarcidae	Ocean pout	*Macrozoarces americanus* (Bloch)	83
Stromateidae	Atlantic butterfish	*Peprilus triacanthus* (Peck)	506
Scorpaenidae	Atlantic redfish	*Sebastes marinus mentella* (L.)	402
Cottidae	Atlantic sea raven	*Hemitripterus americanus* (Gmelin)	19
	Longhorn sculpin	*Myoxocephalus octodecemspinosus* (Mitchill)	240
Bothidae	Fourspot flounder	*Paralichthys oblongus* (Mitchill)	126
Pleuronectidae	American plaice	*Hippoglossoides platessoides* (Fabricius)	767
	Yellowtail flounder	*Limanda ferruginea (Storer)*	1,784
	Winter flounder	*Pseudopleuronectes americanus* (Walbaum)	106
Lophiidae	American angler	*Lophius americanus* Valenciennes	76
		Total: 27 species	26,542

adjacent areas of Subareas 5 and 6, the fishes may generally be divided in three groups according to their usual habitat, i.e. pelagic, near-bottom and bottom-living types (Table 2). It should be noted that this division of fishes into broad groups according to their habitat is arbitrary to a certain extent.

For this analysis of the feeding spectra of fishes which inhabit the area under study, the predators were classified into four groups according to their diet: (i) consumers of mesoplankton and macroplankton, (ii) consumers of nekton, (iii) consumers of benthos and nektobenthos, and (iv) consumers of a broad mixture

TABLE 2. Changes in average annual biomass of various fish populations in Georges Bank and adjacent waters from 1963–65 to 1972–74. (From Edwards and Bowman, MS 1979.)

Species	Average biomass (000 tons) 1963–65	1968–69	1972–74
Alewife	102 (15)[a]	43 (14)[a]	29 (18)[a]
Atlantic argentine	26 (21)	11 (22)	8 (21)
Atlantic butterfish	148 (11)	168 (10)	160 (9)
Atlantic herring	3,566 (1)	1,137 (2)	310 (4)
Atlantic mackerel	472 (5)	3,266 (1)	1,410 (1)
Atlantic redfish	165 (9)	287 (6)	195 (7)
Pollock	216 (8)	213 (8)	245 (5)
Pelagic fish total	4,695	5,125	2,357
Atlantic cod	156 (10)	106 (11)	141 (10)
Red hake	279 (6)	186 (9)	84 (12)
Silver hake	999 (3)	414 (4)	523 (2)
White hake	35 (20)	50 (13)	72 (14)
Spiny dogfish	1,002 (2)	1,024 (3)	362 (3)
Near-bottom fish total	2,471	1,780	1,182
Little skate	146 (12)	43 (15)	97 (11)
Thorny skate	272 (7)	289 (5)	236 (6)
Winter skate	129 (13)	40 (16)	83 (13)
Haddock	783 (4)	254 (7)	161 (8)
Oceanpout	105 (14)	36 (20)	27 (20)
Atlantic sea raven	3 (24)	1 (24)	2 (24)
Longhorn sculpin	11 (22)	18 (21)	7 (22)
American plaice	64 (19)	39 (17)	28 (19)
Fourspot flounder	9 (23)	4 (23)	5 (23)
Winter flounder	71 (18)	36 (19)	38 (17)
Yellowtail flounder	77 (16)	94 (12)	41 (16)
American angler	74 (17)	37 (18)	47 (15)
Bottom fish total	1,744	891	772
Other fish total	810	869	1,039
Grand total	9,720	8,665	5,350

[a]Numerical ranking of species in parentheses.

of organisms. The percentages (by weight) of the major food components of the diets of various fishes arranged by these groups are given in Table 3.

The pelagic species (Group I) primarily consumed planktonic organisms (>90% by weight). The food was composed principally of crustaceans, mainly euphausiids (*Meganyctiphanes norvegica*) and copepods (*Calanus finmarchicus*) and to a lesser extent hyperiids (*Hyperia galla*) and larval decapods. Other planktonic organisms were chaetognaths (*Sagitta elegans*), pteropods (*Limacina retroversa*) and salps (*Salpa* sp.).

The five fishes, classified as consumers of nekton (Table 3, Group II), fed mainly on fish and squids (64–96% by weight), although white hake and silver hake also fed on planktonic crustaceans. The squids consumed by this group were the two species prevalent in the region, namely *Loligo pealei* and *Illex illecebrosus*, with the latter being predominant. The fish prey consisted of representatives of all four groups (Table 3), with red hake, silver hake, Atlantic herring and Atlantic mackerel being generally predominant in the diet. However, the American angler and Atlantic sea raven consumed such bottom fishes as longhorn sculpin and flatfishes in addition to silver hake and red hake. The bottom and near-bottom fishes of this group are mobile and they frequently migrate off the bottom to feed. It is not surprising, therefore, to find pelagic fishes and planktonic organisms in their stomachs. It should also be noted that the proportion of fish taken as food varies with size and age of the predators, and this is especially evident in the case of the hakes.

The eight fishes, classified as Group III consumers (Table 3), fed mainly on benthic and nektobenthic organisms (>82% by weight), and on detritus (87%) in the case of thorny skate. Except for haddock, which fed mainly on echinoderms (63%), and thorny skate, these fishes fed mainly on benthic crustaceans (55–84%) and to a lesser extent on polychaetes, although the latter were important as food for winter flounder, yellowtail flounder and little skate. Fish was a relatively insignificant component of the diet of this group, and planktonic crustaceans were rarely found.

The fourth group of fishes (Table 3) was characterized by a diverse array of prey types. Atlantic cod and red hake, with similar diets, commonly fed on crustaceans (gammarids and shrimps) and fish, and to a much lesser extent on squids, other molluscs and planktonic crustaceans. Pollock, on the other hand, fed mainly on planktonic crustaceans (euphausiids and mysids) and fish. American plaice fed on fish and a variety of benthic organisms, especially echinoderms. Fourspot flounder fed mainly on benthic crustaceans but also on fish.

The percentages of the various fish species utilized as food primarily by Group II and secondarily by Group IV consumers (Table 3) are given in Table 4. Most of the Group II consumers (62–94% fish food) had a preference for silver hake and red hake, although Atlantic herring was an important component of the diets of Atlantic sea raven and spiny dogfish. Additionally, silver hake fed on Atlantic mackerel, American angler fed on sculpins, and white hake fed on wrymouths. Relatively smaller proportions of fish (26–40%) were eaten by the Group IV consumers, most of which also showed a preference for silver hake as food, but American plaice fed mainly on sand lance. Among the Group II and Group IV consumers, the American angler exhibited the greatest diversity of fish food in its diet.

Of the 24 fish species whose average biomass are listed for 1972–74 (Table 2), the five most abundant species in the study area (Atlantic mackerel, silver hake, spiny dogfish, Atlantic herring and pollock) are pelagic or are the more mobile of the near-bottom

TABLE 3. Percentage food composition (by weight) of four groups of consumers in Georges Bank and adjacent waters, 1968–74.

Consumers	Plankton[a]		Benthos and nektobenthos[a]				Nekton[a]		Other food[b]
	CRU	Other	PCH	CRU	MOL	ECH	FIS	SQU	
Group I (consumers of plankton)									
Alewife	56	37	+	7	—	—	—	—	—
Atlantic argentine	97	3	—	—	—	—	—	—	—
Atlantic butterfish	46	53	+	1	—	—	—	—	—
Atlantic herring	89	11	—	+	—	—	—	—	—
Atlantic mackerel	84	14	+	2	—	—	—	+	+
Atlantic redfish	100	—	—	—	—	—	—	—	—
Blueback herring	78	22	—	—	—	—	—	—	—
Round herring	85	9	—	6	—	—	—	—	—
Group II (consumers of nekton)									
American angler	—	—	—	+	—	—	62	38	—
Atlantic sea raven	—	—	—	6	—	—	94	—	—
Spiny dogfish	4	—	—	+	—	—	78	18	—
Silver hake	17	—	+	2	+	—	75	6	+
White hake	25	—	+	10	1	+	64	+	—
Group III (consumers of benthos)									
Little skate	7	—	22	60	—	+	11	—	+
Thorny skate	—	—	3	5	—	—	5	—	87
Winter skate	—	—	19	79	—	—	2	—	—
Haddock	1	—	5	12	2	63	2	9	6
Ocean pout	—	—	11	71	+	7	9	—	2
Longhorn sculpin	3	—	9	84	4	—	—	—	—
Winter flounder	—	—	45	55	—	—	—	—	—
Yellowtail flounder	3	—	27	58	+	1	—	+	11
Group IV (consumers of mixed food)									
Atlantic cod	8	—	2	38	6	4	26	15	1
Pollock	70	—	—	—	—	—	30	—	—
Red hake	6	—	2	44	6	1	26	7	8
American plaice	+	—	6	6	10	22	40	—	16
Fourspot flounder	—	—	—	74	—	—	26	—	—

[a] CRU = crustaceans, PCH = polychaetes, MOL = molluscs, ECH = echinoderms, FIS = fish, SQU = squids.
[b] Other food includes detritus and unidentified remains of fish and invertebrates.

TABLE 4. Percentage composition of various species of ichthyofauna in the food of Group II and Group IV consumers (Table 3) in Georges Bank and adjacent waters, 1968–74.

Fish consumers	Percent (by weight) of fish as food[a]													No. of fish
	BBH	HER	MAC	HKR	HKS	PLA	RED	SAN	SCU	WRY	Other	NS	Total	
Group II consumers														
American angler	7	—	—	7	15	6	3	—	16	—	5	3	62	76
Atlantic sea raven	—	32	—	42	20	—	—	—	—	—	—	—	94	19
Spiny dogfish	—	28	—	12	—	—	1	—	1	—	2	34	78	815
Silver hake	—	2	24	9	34	—	—	1	—	—	1	4	75	7,649
White hake	—	—	—	—	51	—	—	—	—	13	—	+	64	88
Group IV consumers														
Atlantic cod	—	3	3	7	10	1	—	—	+	—	+	2	26	537
Pollock	—	—	—	—	30	—	—	—	—	—	—	—	30	97
Red hake	—	—	—	2	15	—	—	—	—	—	2	7	26	3,848
American plaice	—	—	—	—	+	—	—	40	—	—	—	+	40	767
Fourspot flounder	—	—	—	—	3	—	—	—	—	—	—	23	26	126

[a] BBH = blueback herring, HER = Atlantic herring, MAC = Atlantic mackerel, HKR = red hake, HKS = silver hake, PLA = American plaice, RED = Atlantic redfish, SAN = sand lance, SCU = sculpins, WRY = wrymouth, NS = not specified, and Other = alewife, conger eel, fourbeard rockling, tilefish and butterfish.

fishes (Table 3), and their food consisted mainly of planktonic organisms and nekton. The food resources of pelagic fishes may fluctuate greatly, depending on the pecularities of circulation (Sigaev, 1978) or the transport of numerous macroplankton and mesoplankton from the Gulf of Maine to Georges Bank, the main feeding area for plankton-eaters (Cohen, 1976). Populations of most species which live on or near the bottom (e.g. Atlantic cod, haddock, white hake, skates, sculpin, flatfishes, etc.) usually are considerably smaller than those of the pelagic species. These groundfishes fed mainly on benthos and nektobenthos. The lack of substantial benthic biomass apparently influences the abundance of groundfish (Wigley, 1956). Therefore, few of the benthophagous species achieve large population sizes.

Silver hake and red hake fall into different groups according to their feeding patterns (Table 3). Nektonic organisms (mainly fish, 75%) were dominant in the food of adult silver hake, whereas red hake consumed primarily a variety of bottom and near-bottom invertebrates. Only 33% of the red hake diet consisted of fish and squid. However, the diets of young silver hake and young red hake were similar, with plankton being the preferred food.

Comparison between the FS-coefficients of young silver hake and red hake and the plankton-eaters, such as Atlantic herring and Atlantic mackerel, on the northwestern part of Georges Bank where all four species tend to aggregate during certain times of the year (Table 5), indicated considerable food similarity between young silver hake (11-25 cm) and adult herring and between young red hake (16-25 cm) and young silver hake in both 1971 and 1972, and between young red hake and adult herring in 1971. Although *Meganyctiphanes norvegica* was common as food for all four species, the increased consumption of this euphausiid by young silver hake and herring in 1972 accounted for the increased FS-coefficient for these species. Part of the similarity between young silver hake and young red hake was due to feeding on *Crangon septemspinosa*, and the decrease in FS-coefficient from 1971 to 1972 was due mainly to eating less shrimp. The diets of herring and mackerel were quite similar in both years, but the decline in FS-coefficient from 1971 to 1972 was due to smaller quantities of *Calanus finmarchicus* in their diets. Because euphausiids and copepods are extremely abundant on Georges Bank, it is unlikely that competition for food among adult herring and mackerel and juvenile hakes are pronounced. The large biomass of each of these species during 1972-74 tends to support this view (Edwards, 1976). However, in the case of herring and mackerel, one species may flourish during certain years with a concomitant decrease in abundance of the other (Grosslein *et al.*, 1980). Thus, a decrease in abundance of herring in recent years may have favored the increase in abundance of mackerel, due possibly to increased food resource for the latter species, although the decline in herring abundance may not have been a direct result of an inadequate food supply.

The FS-coefficients, derived from the prey compositions of adult silver hake, red hake, and some other near-bottom and bottom fishes sampled on Georges Bank in June 1971 and 1972, were rather low for most of the comparisons (Table 6). This may be attributed directly to the large differences in prey selected by the predators. The highest similarity (FS = 61) was found between silver hake and white hake in June 1972, when young silver hake was the predominant food of both species. Although the degree of similarity was considerably higher in 1971 than in 1972 for some comparisions, none of the remaining FS-coefficients exceeded 30.

From an analysis of the food composition of fish consumers preying on fishes on Georges Bank in the summer of 1972 (Table 7), the highest FS-coefficients ($\geqslant$30) were observed between spiny dogfish and sea raven, between pollock and white hake, and between silver hake and each of pollock, white hake and sea raven. In all instances, young silver hake was the most common prey for these species. A noteworthy feature of these comparisions is the lack of similarity in the diet of American plaice and the diet of each of the other species listed in Table 7.

Sea raven, angler and white hake, as competitors with and predators of silver hake and red hake, apparently do not influence the population sizes of the latter hake species, possibly because the populations of these predators are quite small. However, the dietary similarity between spiny dogfish, whose biomass is

TABLE 5. Dietary similarity (FS-coefficients) of food composition of young silver hake and red hake and adult Atlantic herring and Atlantic mackerel on Georges Bank in June 1971 and June 1972, expressed as 1971/1972.

Species	Young silver hake	Young red hake	Atlantic mackerel
Atlantic herring	31/49	26/0	52/41
Young silver hake		44/28	13/1
Young red hake			13/0

TABLE 6. Dietary similarity (FS-coefficients) of food composition of adult gadids and yellowtail flounder on Georges Bank in June 1971 and June 1972, expressed as 1971/1972.

Species	HKR	HKW	COD	HAD	YEL[a]
Silver hake (HKS)	18/7	-/61	6/16	22/4	1/1
Red hake (HKR)		-/8	28/14	29/8	18/8
White hake (HKW)			-/14	0/2	0/1
Atlantic cod (COD)				3/17	0/4
Haddock (HAD)					4/6

[a] Yellowtail flounder

TABLE 7. Dietary similarity of food composition (FS-coefficients) of fish consumers preying on fishes on Georges Bank in the summer of 1972.

Species	COD	HKS	POL	HKW	HKR	RAV	PLA	ANG[a]
Spiny dogfish (DGS)	10	11	0	0	02	40	0	9
Atlantic cod (COD)		22	10	10	12	20	0	18
Silver hake (HKS)			30	34	18	31	1	22
Pollock (POL)				30	15	20	0	15
White hake (HKW)					15	20	0	15
Red hake (HKR)						17	0	17
Sea raven (RAV)							0	22
Amer. plaice (PLA)								0

[a] American angler

high, and both silver hake and red hake is low (Table 7), and the feeding of spiny dogfish on these species is of little consequence (red hake and silver hake constituted 12% and 0% of spiny dogfish food respectively) (Table 4). On Georges Bank, the most complex food relationships appear to exist between the two hakes (silver and red) and other gadids (cod, haddock and pollock), whose combined biomass is close to that of silver hake and red hake. It is possible that the trophic impact of cod, haddock and pollock (being cold-water species) on the populations of silver hake and red hake, and on their food resources, increases during periods when the influence of the Gulf Stream on Georges Bank water temperatures is lessened, and decreases during years when warming trends predominate and the abundance of subarctic species declines (Sauskan, MS 1966).

Differences in the trophic relationships of silver hake and red hake become obvious when the feeding spectra of the Georges Bank and southern New England populations of these species are examined separately (Table 8). On Georges Bank, silver hake production depended mainly on pelagic food resources (plankton and nekton), whereas red hake production was derived largely from near-bottom and bottom resources (nektobenthos and benthos). In the southern New England area, the diet of silver hake consisted almost entirely of nektonic organisms (92%), with significant decline in the importance of plankton (euphausiids). Relative to the Georges Bank situation, the diet of red hake in the southern area was much less dependent on plankton (euphausiids) and some nektoplankton (gammarids, shrimps) and more dependent on bottom organisms (sipunculoids, clams, crabs, squid). In both areas, the variety of food types was smaller for silver hake then for red hake. Thus, although silver hake and red hake live under similar conditions of habitat during most of their life cycles and are affected by homogeneous ecological factors, production of these species depends on different ecological groups of animals at least during the post-juvenile period: pelagic organisms for silver hake, and benthic-related organisms for red hake.

Silver hake (mainly a fish-eater) may achieve large biomass and production due to an abundance of food resources, such as young fishes and a great number of planktonic crustaceans (especially euphausiids). Red hake, on the other hand, with mixed type of feeding, have smaller food resources available in the area under investigation, because the food consists largely of bottom and near-bottom invertebrates, the majority of

TABLE 8. Food composition (% by weight) of silver hake and red hake from the Georges Bank and Southern New England areas.

		Georges Bank		S New England	
Food components		Silver hake	Red hake	Silver hake	Red hake
Actinia		—	0.1	—	—
Polychaeta		0.5	2.1	+	0.9
Sipunculoidea		—	0.7	—	19.0
Gammaridae		0.2	17.8	0.3	7.3
Caprellidea		—	0.8	—	1.5
Euphausiidae		28.4	11.6	3.4	2.4
Natantia (shrimps)		2.0	21.2	4.6	9.4
Paguridae (hermit crabs)		—	6.5	+	1.1
Brachyura (crabs)		+	8.5	0.1	12.5
Other crustaceans		0.1	4.4	0.1	1.1
Gastropoda		—	1.3	—	—
Pelecypoda (clams)		—	3.0	—	6.0
Cephalopoda		6.6	3.5	7.7	9.1
Ophiurae		—	0.7	—	—
Holothuriae		—	—	—	1.9
Total invertebrates		37.8	82.2	16.2	72.2
Atlantic herring		5.3	—	0.3	—
Round herring		0.5	—	0.2	—
Silver hake		31.6	4.9	41.9	3.5
Red hake		3.6	0.1	10.0	3.8
Sand lance		+	—	3.0	—
Atlantic mackerel		16.6	—	20.8	—
Atlantic butterfish		0.4	—	2.9	0.7
American plaice		+	0.2	0.1	—
Other fish		3.4	12.5	4.6	5.8
Unidentified fish		—	—	—	14.0
Fish eggs		—	0.1	—	—
Total fish		61.4	17.8	83.8	27.8
Digested food		0.8	—	+	—
Percent:	Plankton	29	12	3	4
	Nekton	68	21	92	23
	Nektobenthos	2	42	5	17
	Bethos	1	25	+	56
Number of food organisms		38	46	31	49
Total number of stomachs		4,416	1,956	3,233	1,892
Percent empty stomachs		36	21	40	20

which are detritophagous animals. The rocky and sandy bottom on Georges Bank indicates low accumulation of detritus and consequent low production of benthos. These factors influence the size of the red hake biomass and production which, according to Edwards and Bowman (MS 1979), is 3–6 times lower than that of silver hake.

The schemes of trophic relations for silver hake and red hake (Fig. 2) were constructed in the manner suggested by Zenkevich (1951) for pelagic and groundfish species of the Barents Sea and by Parin (1971) for pelagic fishes of the open ocean. The position of different food organisms for silver hake and red hake and other fishes in the trophic chains were determined by the feeding patterns of these organisms (Yablonskaya, 1976). Salps, copepods and some euphausiids feed mainly on phytoplankton. Gastropods, cephalopods, sagitta, hyperiids, euphausiids (mainly *Meganyctiphanes norvegica*), and plankton-eating fishes feed mainly on zooplankton. Polychaetes feed predominately on small crustaceans, molluscs, annelid worms, hydroids and sponges (Zernov, 1934). The group of detritophagous animals is represented by some species of polychaetes, clams, echinoderms, as well as shrimps, crabs, gammarids and mysids.

As indicated in Fig. 2A, the energy of silver hake begins with phytoplankton (producers) and extends to crustaceans (consumers of the first and second orders) and then to fishes (consumers of the second and third orders). Detritus is only partly utilized by silver hake through feeding on shrimps, crabs and gammarids. Meanwhile, silver hake is food for white hake, pollock, silver hake, spiny dogfish and American angler, which occupy the third and fourth trophic levels and are consumers of the second and third orders. Silver hake at an early age is a plankton-eater and it then becomes a nektophage (consumer of the second and third orders) as it grows from the juvenile to the adult phase of its life cycle.

Unlike silver hake, red hake utilizes the energy of both phytoplankton and detritus, the detrital branch being of greater importance than that of phytoplankton (Fig. 2B). The detritophagous organisms, on which red hake and the prey of red hake feed, occupy the lower trophic level and are consumers of the second order. Although detritus is not newly-formed (primary) organic matter but is rather a product (remains) of vital activity of organisms at different trophic levels, detritophagous animals may be regarded relatively as primary consumers (Yablonskaya, 1974).

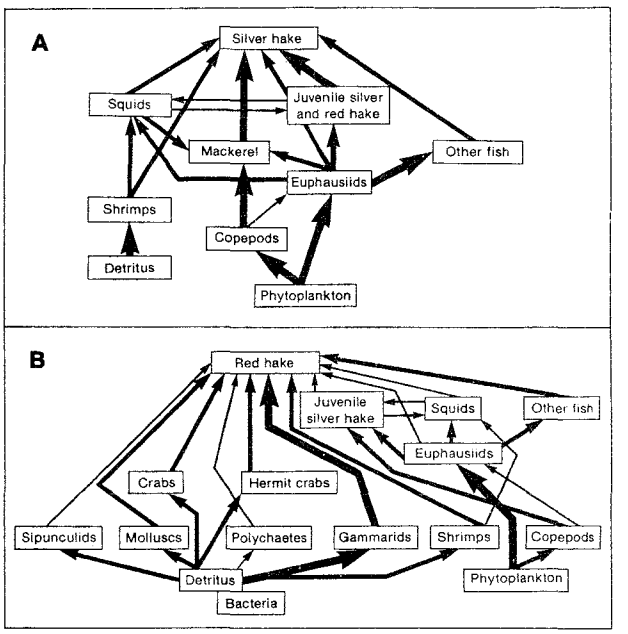

Fig. 2. Schematic illustration of food relations of (**A**) silver hake and (**B**) red hake in the Northwest Atlantic. The thickness of the lines is a quantitative indicator of the importance of the various food organisms.

Summary

The feeding spectra of young silver hake and red hake and adult herring and mackerel on Georges Bank and in adjacent areas are similar, in that they feed mainly on euphausiids. However, in view of the abundance of copepods and euphausiids in the region, competition for food between adult herring and mackerel on the one hand and young silver hake and red hake on the other are unlikely to influence the population size of either species. Food relations (competition, predator-prey relations) are not strongly pronounced between adult silver hake and red hake and other gadids (pollock, cod, haddock). The relatively small populations of fish in the stomachs of pollock and cod, the benthophagous feeding of haddock, and the low abundance of other consumers (sea raven, angler, white hake) of young silver hake and red hake favors the production of silver hake, which is the most numerous consumer of its own young and young red hake. However, the abundance of pelagic food resources (euphausiids, pelagic fishes) in the region under consideration enables the silver hake population to achieve a level several times greater than that of red hake, whose production depends largely on energy provided by detritus through the consumption of bottom and near-bottom invertebrates.

The food chain of silver hake, which occupies the third and fourth trophic levels, extends from phytoplankton to phytophagous and carnivorous crustaceans (consumers of the first and second orders) and to fishes (consumers of the second and third orders). Red hake occupies the third trophic level, with the food chain extending mainly from detritus to detritophagous animals and then to red hake.

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