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Diet of Silver Hake (*Merluccius bilinearis*) on the Scotian Shelf

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Abstract

Predation or competition for similar food resources by silver hake (*Merluccius bilinearis*) has been reported to be associated with the decline in certain gadoid stocks off the northeastern USA. Speculation that the same mechanism may be active on the Scotian Shelf was investigated. The diet of silver hake found off New England and the Scotian Shelf were similar, however, the role of other gadoids such as haddock and cod in the diet of Scotian Shelf silver hake was not as important as that assumed for the New England area. Cannibalism was observed and believed to play a significant role in the regulation of this species. Silver hake on the Scotian Shelf were opportunistic predators preying heavily on crustaceans and fish. The diet was found to be predominantly invertebrates for ages 1-3, while after age 3 was largely fish. There appeared to be little differences in diet composition between males and females. Overall, the diet changed from one largely composed of fish in the spring and autumn to a mixed diet of fish, crustaceans and molluscs during the summer. There were differences in the diet composition at age during the three seasons studied, however, these changes seemed to reflect more the diet of younger *versus* older fish.

Introduction

Silver hake (*Merluccius bilinearis*) occurs in the Northwest Atlantic from the Grand Banks to Cape Hatteras with major centres of abundance on the Central Scotian Shelf, Gulf of Maine, Georges Bank down to Cape Hatteras. Silver hake feeding habits were first reported by USSR scientists based on samples collected in the 1960s throughout its geographic distribution area (Sauskan, MS 1964, Sarnits and Sauskan, 1967; Vinogradov, 1972). Further studies were reported on the basis of collections in 1969-72 and 1973-76 by USA scientists (Bowman, 1975; Maurer, MS, 1975; Langton and Bowman, 1980; Bowman , MS 1980a; b; Durbin *et al*., 1983). These study areas extended from Cape Hatteras to the western Scotian Shelf but excluded the main concentrations on the Scotian Shelf. Clay *et al*. (MS 1984) and Swan and Clay (MS 1979) described food composition of the Scotian Shelf population from 1976 to 1980. The majority of their samples were from the autumn of those years.

The primary conclusions based on the USA data were that fish dominated the diet of silver hake in the New England-mid Atlantic Bight area and that cannibalism was important in certain parts of the area. There was little direct evidence of predation on commercially important species such as cod, haddock and pollock. Since a large portion of the ingested fish was not identifiable, predation on these species may have occurred. Conversely, samples from the Scotian Shelf had the highest percentage of gadoids in the diet. However, there were minimal occurrences of cannibalism compared to other sampled areas. These uncertainties allowed Cohen *et al*. (1982) to speculate that much of the consumption of silver hake could be juveniles of other commercial species and that silver hake predation was an important factor and control of recruitment levels of other important species.

The results of the USA and USSR studies were not easily compared because of the methods used to express stomach contents. However, the USSR studies also showed the predominance of fish in the diet of silver hake in southern waters, while on the Scotian Shelf euphausiids were much more important for smaller silver hake and fish still predominated the diet of the larger silver hake. The data of Swan and Clay (MS 1979) confirmed this areal difference in the diet of Scotian Shelf silver hake. These studies supported the contention that silver hake predation could influence the populations of other fish species such as cod and haddock.

The purposes of the present study were to more thoroughly describe the diet of silver hake on the Scotian Shelf, to determine if there is a possible difference in diet from more southern populations, and to provide an information base on the extent of cannibalism and of predation on other commercial species, particularly other gadoids. The knowledge of those parameters would be useful in subsequent analyses of the dynamics of these populations. Also, these data will be beneficial in comparisons

with similar data for other species in the area to identify cases of diet overlap and potential competition for food.

Materials and Methods

Silver hake were collected between 1981 and 1986 from the Scotian Shelf during several research vessel surveys and from the Canadian as well as the non-Canadian offshore commercial trawler fleets (Fig. 1 and Table 1). Research vessels used a random sampling design stratified by depth (Halliday and Koeller, 1981). The Canadian commercial fleet primarily fished the shallow areas of the Scotian Shelf taking silver hake as by-catch to other species, while the non-Canadian fleets fished for silver hake along the shelf slope during April to June.

Stomach samples were collected using a random sampling design, stratified to fish size, area, season and time of day. Adequacy of sample size in each stratum was evaluated by plotting the cumulative number of prey types. The point at which the curve levels off indicated the minimum number of samples required to represent the entire food array of a particular stratum (Hurtubia, 1973; Cailliet, 1977; Cailliet *et al*. 1986). This procedure suggested a minimal sampling level of 25 specimens for each stratum.

Fork length, weight and sex were recorded for each sampled fish, and otoliths were collected for ageing. Stomachs containing prey were excised aboard the vessel. A cinch tag (Floy Tag Manufacturing, Inc., Model FT-4) was applied to the oesophagus and then the stomach was cut free of the body at the anterior end of the tag and posterior to the pyloric sphincter valve. To arrest further digestion, the excised stomachs were immediately injected with a solution of 10% buffered formalin. These tagged stomachs were then stored in 10% buffered formalin for further examination in the laboratory.

In the laboratory, stomachs were opened, and the contents emptied onto a fine meshed sieve (10μ) and washed. Stomach contents were sorted to the lowest possible taxa. Each taxonomic group was blotted dry and immediately weighed to ±0.01g.

The food composition of the sampled population was calculated as the percent weight of all prey items consumed (%W), i.e. the weight of each prey item expressed as a percentage of the total weight of all prey items in the stomach, and as the percent frequency of occurrence (%F), i.e. the frequency that a prey was found in the stomachs of all sampled fish.

Results

Samples were collected between February and November (1981-86), primarily from NAFO Div. 4W (Fig. 1) with most being taken from May to August in 1982-84 (Table 1). A total of 2 855 silver hake

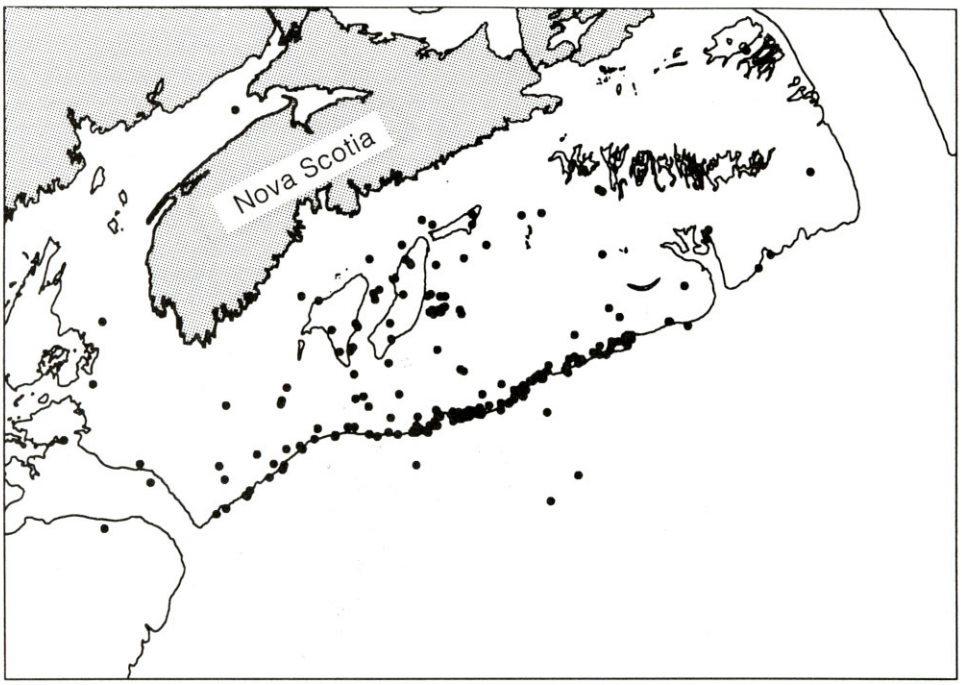

Fig. 1. Locations where silver hake stomach samples were collected.

TABLE 1. Number of silver hake stomachs examined in the study from 1981 to 1986 in Divisions 4W, 4X and Subdivision 4Vs.

	Month									
Area	Feb.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Total
					1981					
4Vs						5				5
4W			8	284	220	452	53			1 017
4X						39	78			117
					1982					
4W			346	8						354
4X			71		1			1		73
					1983					
4Vs								27		27
4W		58	81	337	18	126	58	22		700
4X				21					8	29
					1984					
4Vs								25		25
4W			48	88	25	17		78		256
4X								62		62
					1985					
4Vs		4								4
4W			1	24	40					65
					1986					
4W	121									121
Total	121	62	555	762	304	639	189	215	8	2 855

stomachs were examined, of which 2 173 contained some food. Crustaceans (44%), especially the euphausiid, *Meganyctiphanes norvegica* (19%), were the most frequently occurring prey item (Table 2 and Fig. 2). Fish species were the next most frequent group occurring in 13% of the stomachs with the most frequently occurring species being lantern fish (Myctophidae) (2%) followed by silver hake (2%). Unidentified fish accounted for 8%. By weight, fish constituted the largest portion of the diet (48%). Cannibalism accounted for 25% of the diet by weight, and unidentified fish accounted for 15%. By weight the squid (*Illex illecebrosus*) constituted the second largest prey item in the diet (21%) but occurred with a frequency of only 2%. Crustaceans constituted 20% by weight with *M. norvegica* contributing 13% of the diet. In addition to identifiable food items, there were unidentified remains, including rocks and mucus (frequency of 38%) but constituted only 5% by weight to the overall contents.

The diet composition of 733 males and 1 415 females was determined. Overall, crustaceans rated highest making up 48% of the total weight of all prey in the diet of male silver hake (Table 3), and *M. norvegica* represented 30% by weight of the crustaceans ingested. The weight of fish consumed was half that of crustaceans and was composed mainly of myctophids (8%) and silver hake (7%). Molluscs represented 17% of the diet by weight with *I. illecebrosus* constituting 16%.

Crustaceans ranked highest in frequency of occurrence in the diet of females, but their overall contribution by weight (16%) was considerably less than in the case of males. Fish (53%) especially silver hake (29%), represented a large portion of the female silver hake diet by weight. Females generally consumed two times the amount by weight of fish prey as males. Most notable, the ingestion of *I. illecebrosus* (21%) and silver hake (29%) was greater for females.

Differences in diet composition between males and females were expected, since after age 5 females constitute over 70% of the population (Waldron *et al.*, MS 1991). Thus, diet seemed to be more closely linked to size rather than sex as shown in the Fig. 3. Overall, when silver hake were less than age 4, the diet was largely composed of invertebrate species while fish became more important from age 4 on.

TABLE 2. Silver hake stomach contents in percent occurrence and percent weight by selected prey group.

Prey group	Occurrence (%)	Weight (%)
Pisces	13.1	48.5
Redfish	*	0.1
Lantern fish	2.3	2.3
Other Myctophidae	0.1	0.2
Paralepididae	0.3	1.1
Misc. Pisces	0.2	0.9
Sand lance	0.5	2.3
Cod	*	0.1
Haddock	*	0.2
Silver hake	1.7	25.4
Other Gadidae	0.2	1.3
Unidentified Pisces	7.7	14.7
Fish Eggs	0.1	0.2
Crustacea	43.5	20.3
M. norvegica	19.0	13.1
Other euphausiids	10.4	3.0
Pasiphaeidae	4.8	3.0
Pandalidae	1.9	0.8
Hyperiidae	4.5	0.3
Other Amphipoda	1.2	*
Copepoda	0.6	*
Other Decapoda	0.6	*
Other Crustacea	0.5	*
Polychaeta	0.1	*
Maldanidae	0.1	*
Mollusca	2.9	23.5
Loligo pealei	1.1	2.1
Illex illecebrosus	1.6	21.3
Other Mollusca	0.2	*
Echinodermata	0.4	2.2
Holothuroidea	0.3	2.0
Other Echinodermata	0.1	0.2
Cestoda, Trematoda & Nematoda	1.6	*
Unidentified Remains	38.1	5.2
Inorganic materials	0.1	*

* <0.05

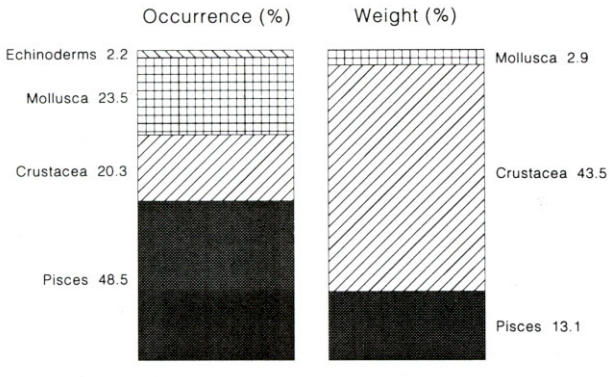

Fig. 2. Diet composition by major prey groups for Scotian Shelf silver hake.

Age specific differences in the silver hake diet are presented in Table 4 and Fig. 4 and 5. Although the number of stomachs representing age group 0 (juveniles) was small (n = 49), it appeared that crustaceans, and in particular, *M. norvegica* constituted most of the diet by weight. Fish prey were present in the diet of these silver hake, unfortunately the fish prey was unidentifiable for this age group.

Age group 1 silver hake (n = 257) fed primarily on crustaceans (W = 79%, F = 56%). Euphausiids comprised most of this category, particularly *M. norvegica* (W = 40%). Fish prey represented only a very small proportion of the diet (W = 9%) of which silver hake (cannibalism) was 3% by weight.

The diet composition of age group 2 (n = 744) seemed to be quite similar to the age group 1. However, ingestion of crustaceans was lower (W = 65%) and was primarily *M. norvegica* (W = 45%). Fish as prey occurred more frequently (10%) and contributed more in terms of weight (17%). Major

TABLE 3. Stomach contents in male and female silver hake given as percent occurrence and percent weight by selected prey groups.

	Male		Female	
Prey group	Occurrence (%)	Weight (%)	Occurrence (%)	Weight (%)
Pisces	11.1	24.7	15.4	53.1
Redfish	*		0.1	0.1
Lantern fish	3.4	7.0	2.0	1.6
Other Myctophidae	0.2	1.4	*	*
Paralepididae	0.2	0.9	0.5	1.2
Misc. Pisces	0.1	0.1	0.3	1.0
Sand lance	0.2	1.5	0.6	2.5
Cod	0.1	0.1	*	0.1
Haddock	*		*	0.2
Silver hake	0.4	6.7	2.6	28.8
Other Gadidae	0.2	1.7	0.2	1.2
Unidentified Pisces	6.4	5.3	9.2	16.4
Fish Eggs	*		0.1	0.2
Crustacea	49.9	47.9	39.5	16.0
M. norvegica	22.0	29.7	17.8	10.6
Other euphausiids	10.6	6.3	8.4	2.4
Pasiphaeidae	6.1	7.9	4.6	2.2
Pandalidae	2.1	2.4	2.0	0.5
Hyperiidae	6.1	1.1	4.0	0.2
Other Amphipoda	1.0	*	1.1	*
Copepoda	0.8	0.1	0.5	*
Other Decapoda	0.6	0.2	0.6	*
Other Crustacea	0.6	0.2	0.4	*
Polychaeta	0.1	*	0.1	*
Maldanidae	0.3	*	0.1	*
Mollusca	1.6	16.5	3.7	23.6
Loligo pealei	0.7	0.8	1.4	2.3
Illex illecebrosus	0.8	15.7	2.2	21.3
Other Mollusca	0.2	*	*	*
Echinodermata	0.1	1.5	0.7	2.4
Holothuroidea	0.1	1.5	0.5	2.1
Other Echinodermata	*		0.1	0.3
Cestoda, Trematoda & Nematoda	.8	*	1.0	*
Unidentified remains	36.0	9.4	39.4	4.6
Inorganic materials	0.2	*	0.1	*

* <0.05; blank = no observation

contributed more in terms of weight (17%). Major components of this category (by weight) were Myctophidae (10%) and Paralepididae (2%) with 4% of the fish category being unidentifiable. Molluscs represented only a very small portion of the diet (7%); *I. illecebrosus* first appeared as a prey item in this age group. It appeared that there was a trend for older silver hake to consume increasingly larger prey.

A number of important changes were apparent in the diet of age group 3 (n = 299). A switch to larger prey relative to the younger age groups was evident by the increased consumption of fish (W = 26%) and molluscs (W = 9%) resulting in a decline in the presence of crustaceans in the diet (W = 51%). Paralepidids (W = 2%) and myctophids (W = 9%) comprised the bulk of the fish prey. *Meganyctiphanes norvegica* (W = 34%) was still the dominant crustacean consumed, however, *I. illecebrosus* was increasing in importance as a prey item (W = 7%). Ingestion of Holothuroidea (sea cucumbers, W = 5%) suggested that silver hake of this age group were in close proximity to the bottom, at least part of the time, and migrated vertically to obtain pelagic prey.

Further decline in the consumption of crustaceans (W = 34%) was apparent in age group 4 (n = 1 015) with an equal amount of the diet consisting of fish (W = 34%) and an increased diet of molluscs (W = 19%). Cannibalism was most apparent in these

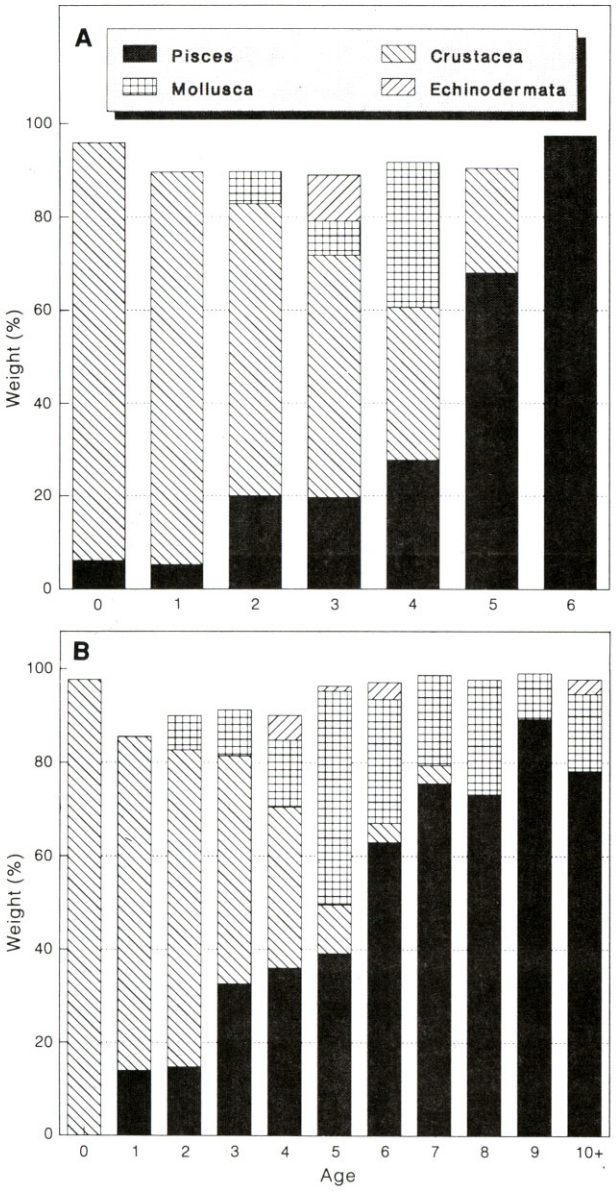

Fig. 3. (**A**) Male and (**B**) female silver hake stomach contents by major prey group and age.

accounted for 9% of their overall diet by weight. Up to 18% of the diet was represented by *I. illecebrosus* and crustaceans were still important with *M. norvegica* contributing 23% by weight.

Crustaceans (W = 11%) decreased in importance while fish species (W = 40%) increased in age group 5 (n = 244). Molluscs (W = 45%) in all cases were the main diet consumed by weight and *I. illecebrosus* was found frequently and constituted the main species consumed by weight (W = 42%). Silver hake, again, was evident as the main fish species in the diet.

The major part of the diet of age group 6 (n = 122) consisted of fish (W = 63%). Silver hake was the single major prey species constituting 31% by weight of total prey consumed. Crustaceans made up only 4% by weight of the diet and *I. illecebrosus* again was the major invertebrate prey.

The diet of silver hake age groups 7–9 were dominated by fish, especially silver hake. *Illex illecebrosus* was again the major invertebrate in the diet. Crustaceans constituted a minor part of age group 7 diet and were infrequently part of the diet of age group 8 and older silver hake.

Considerable variation in the seasonal diet composition of silver hake (Table 5) was assumed to reflect age-specific differences in prey species consumed as well as possible variation in the abundance and availability of these prey organisms. In order to separate seasonal diet variations, prey composition was examined by age-group through most of the year (February–November). Sampling levels, as shown in Table 1 indicate in certain seasons and years, sample sizes were small and provided only a cursory view of the diet.

Table 6 summarizes the number of silver hake stomachs examined for each age by season (spring – March to May, summer – June to August, autumn – September to November). The seasonal number of samples for juvenile silver hake (Table 6A) were minimal and this age group was not included in the analysis.

Temporal changes in diet composition for age group 1 silver hake are summarized in Table 6B and Fig. 6A. In this group, there was a trend for the proportion of crustaceans ingested to increase from spring to summer and then decline to the end of the year. Although seasonal sample sizes were small, the increase in consumption of crustaceans, particulary *M. norvegic*a, during the summer may have reflected an increase in abundance of this prey category, or assuming the opportunistic nature of silver hake predation, a subsequent decline in the abundance of fish prey. Fish as prey represented a relatively larger portion of the diet during spring and autumn but not during summer.

The seasonal diet composition for age group 2 displayed a pattern similar to that observed for age group 1 (Table 6C and Fig. 6B). Fish were generally more important (by weight) as prey from spring to summer declining to the autumn. Within this prey category, Myctophidae and Paralepididae were predominant. Although crustaceans (especially euphausiids), comprised the bulk of the overall diet , their consumption increased from spring to autumn. Molluscs (mainly *I. illecebrosus*) were found in the

TABLE 4 Silver hake stomach contents in percent occurrence (F) and percent weight (W) by prey groups and age.

	Age																					
	0		1		2		3		4		5		6		7		8		9		10	
Prey group	F	W	F	W	F	W	F	W	F	W	F	W	F	W	F	W	F	W	F	W	F	W
Pisces	3 2	5.5	3.3	8.1	10.0	17:2	13.9	25.9	13.2	33.8	17 8	39.9	28.3	63 2	39.6	71.4	33.3	73 2	43.8	86.6	25.7	70.6
Redfish	•		•		•		•		0.1	•	•		0.5	0.6	•		•		•		•	
Lantern Fish	•		•		3.3	7.6	3.9	7.6	2.7	4.8	1 2	0.2	1.0	0.3	•		•		•		•	
Other Myctophidae	•		•		0 2	1.9	0 4	1 0	0.1	0.1	•		•		•		•		•		•	
Paralepididae	•		•		0.2	1 5	0.4	1 7	0.6	3.0	•		0.5	0.5	0.9	0.6	•		•		•	
Misc. Pisces	•		•		0.2	1.0	0 2	1.5	0.2	1.1	•		1.5	3.3	•		•		•		•	
Sand lance	•		•		0.1	0.6	•		0.4	2.1	0.7	2.4	2.4	3.0	5.4	6.5	5.6	2.2	•		•	
Cod	•		•		•		•		0.1	0.1	0.2	0.4	•		•		•		•		•	
Haddock	•		•		•		•		•		•		•		•		•		6.3	3.9	•	
Silver Hake	•		0 5	2.7	0.1	0.6	•		1 0	9.0	4.5	21.5	8.3	31 3	15.3	41.4	11.1	44.3	25.0	79.6	5 7	37.8
Other Gadidae	•		0.5	2 9	0.1	0 3	0.2	0.1	0.1	0.8	0.2	•	•		0.9	7.9	•		•		•	
Unidentified Pisces	3 2	5.5	2.3	2.6	5.9	3.7	8.9	13.9	8 1	12 9	10.9	15 4	14.1	24.0	17.1	15.1	16.7	26.7	12 5	3.1	20.0	32.9
Fish eggs	•		•		0 1	•	•		0.1	0.8	0 2	•	•		•		•		•		•	
Crustacea	87.1	90 5	55.6	78 8	52.3	65.4	43 3	50 5	40.9	34 0	34.1	10.7	23.9	4.1	13.5	3.6	•		6.3	•	5.7	•
M. norvegica	32 3	58.5	19.9	40.3	25.7	45.1	19.3	33.7	17.2	22.8	15 2	6.2	10.7	2.1	6.3	1.0	•		•		2.9	•
Other euphausiids	51 6	29.6	23 7	27.0	10.5	7.1	8.5	7.9	7.4	4 1	8.3	2 1	8.3	1.6	2.7	0.4	•		6.3	•	•	
Pasiphaeidae	3 2	2.4	0 3	1.1	5 6	9.8	5.6	6 4	6.7	4.9	4.3	1.9	2 0	0 2	0.9	2.2	•		•		•	
Pandalidae	•		3.1	8.3	1.8	1.7	1.2	0 6	2.1	1 6	1.7	0 2	2.0	0.2	0.9	•	•		•		•	
Hyperiidae	•		2 9	0 5	6.1	1 5	5.8	0.9	4.7	0.4	3.1	0.3	1.0	0.1	1.8	•	•		•		•	
Other Amphipoda	•		2.6	0.1	1.2	•	1.0	0.1	1.2	•	0.5	•	•		•		•		•		2.9	•
Copepoda	•		1.3	0 2	0.5	0.1	0.8	0.1	0.6	0 1	0.2	•	•		•		•		•		•	
Other Decapoda	•		0.5	0.5	0 7	0.2	0.8	0.4	0.7	•	0.2	•	•		0.9	•	•		•		•	
Other Crustacea	•		1 3	0.8	0.2	•	0.4	0.3	0.4	•	0.7	•	•		•		•		•		•	
Polychaeta	•		0.3	0.1	0 1	•	0.2	•	0.2	•	•		•		•		•		•		•	
Maldanidae	•		•		•		•		0.1	•	•		•		•		•		•		11.4	0.3
Mollusca	•		0 8	•	1.1	7.2	1.4	8 5	2.4	18.5	8.5	44.5	8.8	26.2	9 9	23 6	16.7	24.5	12.5	12 2	14.3	22.2
Loligo pealei	•		•		0.6	1.2	0.8	1.3	1.1	0.7	2.1	2.2	2.4	6.8	4.5	3.1	11.1	0.1	6.3	•	5.7	1.4
Illex illecebrosus	•		•		0.3	5.9	0.4	7.2	1.4	17.9	6.4	42.3	6.3	19.4	5.4	20.5	5.6	24.4	6 3	12.2	5.7	20.8
Other Mullusca	•		0.8	•	0.2	•	0.2	•	•	•	•		•		•		•		•		2.9	•
Enchinodermata	•		•		•		0.2	5.1	0.7	4 2	0.2	1 1	1.0	3.5	0.9	•	•		•		11.4	4.2
Holothuroidea	•		•		•		0.2	5.1	0.6	4.2	0.2	1.1	1.0	3.5	0.9	•	•		•		2.9	•
Other Enchinodermata	•		•		•		•		0.1	•	•		•		•	•	•		•		8.6	4.1
Cestoda, Trematoda & Nematoda	•		6.7	0.2	0.6	•	0.6	•	0.6	•	1.2	•	2.0	•	5.4	•	16.7	•	•		•	
Unidentified remains	9.7	4.0	33.3	12.7	35 8	10 2	40.4	10 0	41 7	8.7	37.9	3.8	36.1	3.0	30.6	1.3	33.3	2.3	37.5	1.2	31.4	2.7

• <0.05; blank = no observation or no data

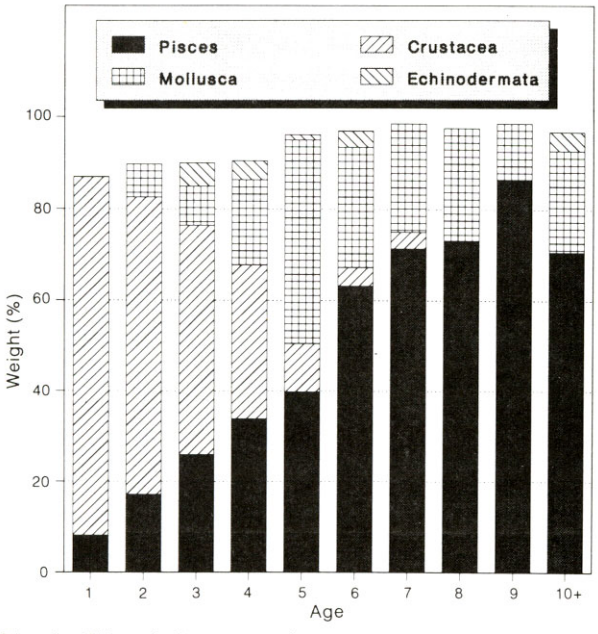

Fig. 4. Silver hake stomach contents as percent weight by major prey group and age.

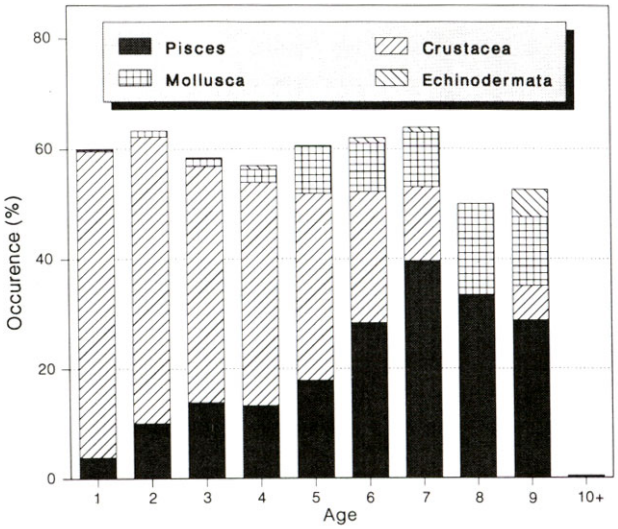

Fig. 5. Silver hake stomach contents as occurence percent by major prey groups by age.

Molluscs (mainly *I. illecebrosus*) were found in the diet throughout the year but were highest in the spring and autumn. The increased diversity in diet composition between the seasons may reflect a higher abundance of "fish" and "Mollusca" prey in the spring.

Considerable variation was apparent in the seasonal diet composition of age group 3 (Table 6D and Fig. 6C). Fish as prey were abundant in the diet in the spring and summer but declined to low levels in the autumn. Myctophidae and Paralepididae were principal contributors to the fish diet. The proportion of crustaceans in the diet by weight increased steadily from spring through to autumn with *M. norvegica* representing the bulk of this category. Molluscs (predominantly *I. illecebrosus*) were present in the diet only in the summer reflecting the increased abundance of *I. illecebrosus* on the Scotian Shelf at that time. Echinoderms (holothuroids) occurred in the diet only in the summer, representing 8% of the diet by weight. Generally, age group 3 silver hake consumed more fish, molluscs and echinoderms than the smaller size groups, however, the number of prey categories in the diet (i.e. diversity) tended to decline from spring through to autumn, when only crustaceans were ingested.

Silver hake age group 4, and older, concentrated much of their feeding on fish and molluscs (cephalopods) (Table 6E and Fig. 6D). The proportion of fish prey in the diet by weight showed a declining trend from spring to summer then increased in the autumn to levels similar to those in the spring. Silver hake juveniles were consumed through the year and represented the bulk of the identifiable fish prey eaten. The proportion of the diet represented by molluscs showed considerable variation, with a maximum occurring in the summer. *Illex illecebrosus* was the major prey consumed in this category. Ingestion of crustaceans also varied extensively, with peak consumption occurring in the summer and autumn. As in the case of age group 3 silver hake, echinoderms (mainly holothuroids) appeared in the diet in spring and summer only. This considerable temporal diet variation apparent in age group 4+ silver hake probably reflected seasonal variation in the availability of the various prey.

Discussion

The limited reporting in earlier studies provide little detail of the 42 000 stomachs analyzed and it makes comparison with those studies difficult. However, frequency of occurrence comparisons were possible. Vinogradov (1972) reported that Euphausiidae were most often found in the stomach of Scotian Shelf silver hake, while fish were the predominant prey in the Georges Bank samples. Also, larger silver hake from the Scotian Shelf were reported to have a diet composed mainly of fish species such as sand lance, argentine, lantern fish and juvenile silver hake.

The USA scientists interested in the trophic biology of commercially important finfish conducted a stomach sampling program which ran from 1969 to 1972. The results were initially reported by Bowman (1975) and Maurer (MS 1975), and in more

TABLE 5. Silver hake stomach contents in percent occurrence and percent weight by selected prey groups for all ages and seasons.

	Spring		Summer		Autumn	
Prey groups	Occurrence (%)	Weight (%)	Occurrence (%)	Weight (%)	Occurrence (%)	Weight (%)
Pisces	15.0	59.8	12.7	29.7	10.2	62.2
Redfish	0.1	0.2	*	*	*	
Lantern fish	2.1	1.1	2.9	4.5	0.2	*
Other Myctophidae	*		0.2	0.6	*	
Paralepididae	0.6	1.6	0.3	0.9	*	
Misc. Pisces	0.1	0.2	0.2	1.1	0.2	2.6
Sand lance	0.2	0.7	0.1	0.4	2.5	12.9
Cod	*		0.1	0.2	*	
Haddock	*		*	0.5	*	
Silver hake	3.5	32.7	0.6	15.1	1.9	29.1
Other Gadidae	0.2	2.6	0.1	*	0.5	0.3
Unidentified Pisces	8.2	20.8	8.1	6.2	5.1	17.4
Fish eggs	0.1	0.4	0.1	*	*	
Crustacea	39.6	9.0	39.9	32.3	68.6	25.6
M. norvegica	16.1	5.1	18.8	22.5	26.9	14.0
Other euphausiids	10.0	0.9	6.3	3.1	29.2	9.7
Pasiphaeidae	6.0	2.1	5.1	5.2	0.8	0.1
Pandalidae	2.3	0.8	1.1	0.5	4.5	1.4
Hyperiidae	2.8	0.1	5.8	0.7	3.1	0.1
Other Amphipoda	1.1	*	1.3	*	1.1	*
Copepoda	0.9	*	0.4	0.1	0.8	*
Other Decapoda	0.1	*	0.8	0.1	0.8	0.1
Other Crustacea	0.4	*	0.3	*	1.6	0.1
Polychaeta	*		*	*	0.9	*
Maldanidae	0.1	*	0.1	*	0.3	0.1
Mollusca	3.3	23.6	3.2	28.7	0.6	8.5
Loligo pealei	0.3	0.4	1.8	3.7	0.3	3.6
Illex illecebrosus	2.7	23.2	1.3	24.9	0.3	4.9
Other Mollusca	0.3	*	0.1	*	*	
Echinodermata	0.4	2.0	0.4	2.6	0.6	1.5
Holothuroidea	0.3	2.0	0.4	2.6	0.2	*
Other Echinodermata	0.1	*	*		0.5	1.5
Cestoda,Trematoda & Nematoda	3.0	*	0.6	*	2.3	*
Unidentified remains	38.4	5.0	43.0	6.7	16.1	2.0
Inorganic materials	0.1	*	*	*	0.2	*

* <0.05; blank = no observation

detail by Langton and Bowman (1980). Another survey conducted from 1973 to 1976, was reported by Bowman (MS 1980b), Bowman and Bowman (1980) and Durbin *et al.* (1983). Both sampling programs were extensive for most finfish species, and covered a large area extending from Cape Hatteras to the western Scotian Shelf.

The USA and USSR results were in agreement showing the major prey in the diet of silver hake were fish and crustaceans. Edwards and Bowman (1979), who first warned of the ecological consequences of uncontrolled expansion in the silver hake population, focused attention on the consumption of other fish species by silver hake. They estimated that silver hake could consume approximately 10% of the standing crop of all fish on Georges Bank and the Gulf of Maine. The major part of that consumption would be small or juvenile fish, implying that silver hake would be the main species regulating the Northwest Atlantic ecosystem. They further stated, "... it is difficult to escape the fact that the species composition of the ecosystem (off New England) is dependent to some significant degree on the population status of silver hake and, to a lesser degree, the spiny dogfish". Edwards and Bowman (1979) went on to postulate that silver hake was instrumental in controlling the recruitment of several species, most notably haddock, herring and Atlantic mackerel prior to 1963. As supportive evidence, they observed that during the period, 1963–74, these three species had unusually large and successful year-classes at a time when the silver hake population was declining. They also

TABLE 6 . Number of silver hake stomachs examined for each age group (0 to 4+) (A to E, respectively) expressed in percent occurrence and percent weight by season.

	Spring		Summer		Autumn	
Prey Groups	Occurrence (%)	Weight (%)	Occurrence (%)	Weight (%)	Occurrence (%)	Weight (%)
			A. Age 0			
Pisces	25.0	12.5				
Crustacea	50.0	79.2			92.6	99.5
M. norvegica	25.0	73.8			33.3	46.1
Other euphausiids					59.3	53.4
Pasiphaeidae	25.0	5.3				
Unidentified remains	25.0	8.4			7.4	0.5
			B. Age 1			
Pisces	2.4	7.3	2.2	0.5	7.0	12.5
Silver hake	0.4	3.6	*		0.9	2.0
Unidentified Pisces	2.0	3.7	2.2	0.5	3.5	1.3
Crustacea	50.7	74.1	64.4	88.8	71.9	83.6
M. norvegica	19.4	42.8	28.9	54.3	18.4	30.5
Other eupausiids	22.7	22.4	22.2	32.7	28.1	33.1
Pasiphaeidae	0.4	1.9	*		*	
Pandalidae	1.5	6.2	2.2	0.8	9.6	14.9
Hyperiidae	1.5	0.5	8.9	0.9	6.1	0.4
Other Amphipoda	3.1	0.2	2.2	*	0.9	0.1
Copepoda	0.9	*	*		3.5	0.7
Other Decapoda	0.2	*	*		1.8	1.4
Other Crustacea	0.9	0.1	*		3.5	2.5
Polychaeta & Maldanidae	*	*	*		1.8	0.4
Mollusca	1.1	*	*		*	
Cestoda, Trematoda & Nematoda	8.8	0.3	*		0.9	*
Unidentified remains	37.0	18.3	33.3	10.7	18.4	3.4
			C. Age 2			
Pisces	11.9	16.8	10.8	20.6	2.5	2.0
Lantern fish	5.1	7.6	3.1	0.2	0.6	0.2
Other Myctophidae	*		0.3	3.0	*	
Paralepididae	*		0.4	2.3	*	
Misc. Pisces	*		0.3	1.5	*	
Unidentified Pisces	6.1	5.1	6.6	3.7	1.9	1.8
Sand lance	0.3	2.9	*		*	
Silver hake	*		0.1	1.0	*	
Fish Eggs	*		0.1	*	*	
Crustacea	50.2	57.6	47.1	64.7	82.3	80.9
M. norvegica	21.2	30.3	24.4	47.6	40.5	56.2
Other euphausiids	6.5	2.8	7.9	5.8	31.0	19.5
Pasiphaeidae	11.3	19.6	4.3	8.3	1.9	1.2
Pandalidae	2.7	3.1	0.9	0.8	4.4	3.6
Hyperiidae	6.1	0.7	6.9	2.0	1.9	0.3
Other Amphipoda	0.3	*	1.5	*	1.3	*
Copepoda	1.7	0.6	0.1	*	*	
Other Decapoda	0.3	0.6	0.9	0.1	0.6	*
Other Crustacea	*		0.3	*	0.6	*
Polychaeta & Maldanidae	*		*		0.6	0.1
Mollusca	0.7	9.3	1.4	4.6	0.6	15.4
Loligo pealei	0.3	0.9	0.9	1.6	*	
Illex illecebrosus	0.3	8.4	0.3	3.0	0.6	15.4
Other Mollusca	*		0.3	*	*	
Cestoda, Trematoda & Nematoda	1.0	*	0.3	*	1.9	*
Unidentified remains	36.2	16.3	40.4	10.1	12.0	1.6
Inorganic materials	1.0	*	*		*	

TABLE 6. Continued.

Prey Groups	Spring Occurrence (%)	Spring Weight (%)	Summer Occurrence (%)	Summer Weight (%)	Autumn Occurrence (%)	Autumn Weight (%)
			D. Age 3			
Pisces	14.0	47.0	15.1	20.6	2.6	0.1
Lantern fish	4.0	4.6	4.2	9.9	*	
Other Myctophidae	*		0.5	1.6	*	
Paralepididae	*		0.5	2.7	*	
Misc. Pisces	*		0.3	2.4	*	
Other Gadidae	*		0.3	0.2	*	
Unidentified Pisces	10.0	42.4	9.3	3.9	2.6	0.1
Crustacea	48.0	43.1	38.4	46.9	79.5	98.7
M. norvegica	20.0	25.6	16.4	30.7	46.2	80.1
Other euphausiids	9.0	6.5	6.9	7.2	23.1	17.3
Pasiphaeidae	12.0	10.0	4.5	5.8	*	
Pandalidae	1.0	0.6	1.1	0.6	2.6	1.1
Hyperiidae	4.0	0.2	6.3	1.3	5.1	0.2
Other Amphipoda	1.0	*	0.8	0.1	2.6	*
Copepoda	1.0	0.2	0.8	0.1	*	
Other Decapoda	*		1.1	0.6	*	
Other Crustacea	*		0.5	0.5	*	
Polychaeta & Maldanidae	*		*		2.6	*
Mollusca	*		1.9	13.3	*	
Loligo pealei	*		1.1	2.1	*	
Illex illecebrosus	*		0.5	11.2	*	
Other Mollusca	*		0.3	*	*	
Holothuroidea	*		0.3	7.9	*	
Cestoda, Trematoda & Nematoda	1.0	*	0.5	*	*	
Unidentified remains	37.0	9.9	43.9	11.3	15.4	1.1
Inorganic materials	1.0	0.1	*		*	
			E. Age 4+			
Pisces	17.6	51.5	13.6	42.9	21.3	78.0
Redfish	0.1	0.2	*		*	
Lantern fish	2.8	1.9	1.3	1.7	*	
Other Myctophidae	0.1	0.1	*		*	
Paralepididae	0.7	1.7	0.1	0.3	*	
Misc. Pisces	0.2	0.7	0.1	0.2	0.5	4.7
Sand lance	0.4	0.9	*		8.1	23.8
Cod	*		0.3	0 .4	*	
Haddock	*		0 .1	0 .8	*	
Silver hake	3.4	24.8	2.2	33.5	2.0	19.9
Unidentified Pisces	9.7	19.1	9.4	5.9	10.7	29.6
Crustacea	38.0	14.2	28.3	15.4	54.8	16.2
M. norvegica	16.7	8.7	13.2	12.5	15.2	4.4
Other euphausiids	4.6	1.3	5.4	0.9	36.5	11.7
Pasiphaeidae	8.3	3.2	0.9	1.3	*	
Pandalidae	2.0	0.7	2.1	0.5	0.5	0.1
Hyperiidae	5.0	0.3	2.2	0.1	1.0	*
Other Amphipoda	0.4	*	2.4	*	*	
Copepoda	0.6	0.1	0.1	*	*	
Other Decapoda	0.2	*	1.3	*	0.5	*
Other Crustacea	0.2	*	0.7	*	1.0	*
Polychaeta & Maldonidae	0.1	*	0.7	*	1.0	0.2
Mollusca	4.6	24.5	5.7	38.7	0.5	0.9
Loligo pealei	1.2	0.9	2.9	6.2	0.5	0.9
Ilex illecebrosus	3.4	23.6	2.6	32.5	*	
Other Mollusca	*		0.1	*	*	
Echinodermata	1.0	3.5	*		2.0	2.8
Holothuroidea	0.9	3.5	*		0.5	*
Other Echinodermata	0.1	*	*		1.5	2.8

TABLE 6. Continued.

Prey Groups	Spring Occurrence (%)	Spring Weight (%)	Summer Occurrence (%)	Summer Weight (%)	Autumn Occurrence (%)	Autumn Weight (%)
Cestoda, Trematoda & Nematodes	0.7	*	0.4	*	5.6	*
Unidentified remains	37.7	5.8	51.1	3.0	14.2	1.5
Inorganic materials	0.1	*	0.1	*	*	

* <0.05; blank = no observation

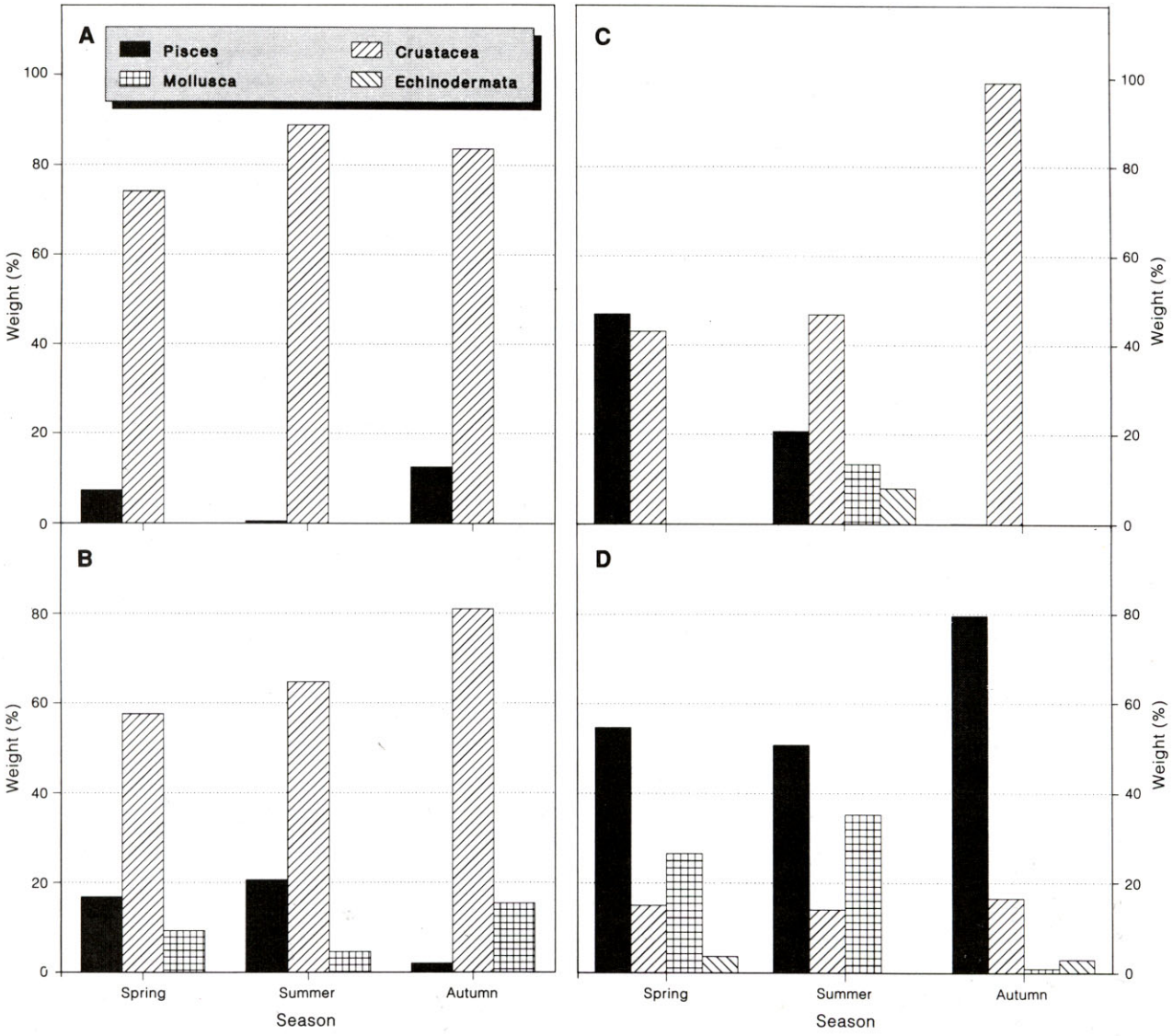

Fig. 6. Seasonal stomach contents for (**A**) age 1; (**B**) age 2; (**C**) age 3; (**D**) age 4+; silver hake by major prey group.

inferred that additional pressure on these populations could have resulted from feeding competition because the abundant juvenile silver hake population fed on invertebrates, especially euphausiids, which form a large part of the diet of other species such as cod and haddock.

Bowman (MS 1980a) indicated that silver hake was an opportunistic predator, the more abundant the prey the more predation by silver hake, and supported of this argument concluding that the increased predation on haddock (*Melanogrammus aeglefinus)* and sand lance (*Ammodytes ameri-*

canus) was related to the exceptionally high recruitment for those two species.

Further work on the role of silver hake in the marine ecosystem off New England was presented by Cohen *et al*. (1982), who calculated the consumption by seven fish species, including silver hake. They concluded that "On Georges Bank it is noteworthy that the consumption of one finfish species, silver hake, exceeds total productivity of the exploited finfish and *Illex* community. Silver hake (like cod and squid) feed heavily on other finfish (Grosslein *et al*., 1980); therefore much of its consumption must be of pre-recruit fish. The impact of pre-recruit consumption of silver hake and other fish predators is unknown, but its potential significance is very great, particularly as its effects might be partially controlled through [fisheries] management".

Based on these trophic studies, fisheries scientists (Bowman, MS 1980a; b; Cohen and Grosslein, 1982; Edwards and Bowman, 1979; Sissenwine *et al*., MS 1983) concluded that silver hake was a major fish predator and suggested that its biomass should be controlled through effective fisheries management. In particular, Edwards and Bowman (1979) suggested that predation on juvenile herring, mackerel and haddock could be extensive, and would inevitably influence the recruitment of these species. These statements on the role of silver hake in the ecosystem set the stage for the introduction of the hypothesis that silver hake is a prime driving force in the marine ecosystem off New England. In particular, predation by the older members of the species could contribute significantly to recruitment failures for species such as haddock.

An obvious question is whether the observations of the trophic behaviour of silver hake presented for adjacent areas can be applied to those found on the Scotian Shelf. Swan and Clay (MS 1979) and Clay *et al*. (MS 1984) noted that Scotian Shelf silver hake less than 30 cm preyed heavily on invertebrate species, while those greater than 30 cm preyed primarily on fish species. Overall they noted that only 8% by weight of the diet was fish. Waldron (MS 1983) also noted the minor importance of fish (2%) in the diet. Both studies reported considerably less than that observed off New England (Langton and Bowman, 1980). The USA studies showed that the proportion of fish consumed varied between 54 and 78% by weight over the sampling area. Samples from the Middle Atlantic Bight had a diet of 54 to 88% fish with cannibalism accounting for 13 to 21% of the diet. The diet of silver hake from Southern New England (62–78%), Georges Bank (78–76%) and the Gulf of Maine (76%) was largely mackerel and silver hake. Cannibalism was 7 to 8% for Southern New England. Little cannibalism (<0.4%) was noted from fish sampled on Georges Bank, however, 78% of the diet was other fish species, notably myctophids which accounted for 3% of the diet. Only 1% of the diet for fish in the Gulf of Maine was silver hake. Estimates for a specific species are underestimated since in all cases, a large proportion of fish prey could not be identified due to the advanced state of digestion. Several researchers have expressed concern that these unidentified fish species could represent post larval stages of various gadoids such as haddock and silver hake (Maurer, MS 1975; Bowman, 1975).

In this study, crustacea occurred most frequently (54%) with the euphausiids, *M. norvegica*, being the main species eaten. In terms of percent by weight, however, fish comprised the major portion of the diet (44% as opposed to 19% for crustaceans), half of which was represented by silver hake (20%). The lower frequency of occurrence of fish in the diet compared to that for Georges Bank, may reflect a difference in the availability of fish as prey compared to crustaceans. Although molluscs rated third in frequency of occurrence, their overall contribution by weight (29%) was second to that of fish, and consisted primarily of the squid *I. illecebrosus*. Langton and Bowman (1980) results agree with those found in this study. From the 1969 to 1972 sampling program they established that the diet of silver hake from the Western Scotian Shelf was mainly fish (W = 65%), in particular gadoids (W = 51%), with crustaceans (W = 34%) represented predominantly by euphausiids (W = 28%). In their study, no molluscs were reported in the diet from this region.

The importance of invertebrate prey on the Scotian Shelf and their lower contribution to the diet of New England silver hake may reflect spatial and temporal differences in prey abundance. Lange (MS 1982) indicates that the abundance of the major squid prey (*Loligo pealei)* was in a rebuilding stage from an all time low in 1971 to a near record high in 1974. Conversely, in the current study, a record high abundance of *I. illecebrosus* was observed. Aside from availability of other prey, there is no apparent reason why squid should be selected as prey on the Scotian Shelf and not off New England.

In the USA study, cannibalism accounted for <1% on Georges Bank to 21% off the Southern New England-Middle Atlantic area, while for the Scotian Shelf, all historical studies report that cannibalism accounted for 1% of the diet by weight. From the data presented here, cannibalism accounted for 25% of the Scotian Shelf silver hake diet by weight (Table 2). The difference between these studies

could be related to prey abundance. Almeida and Anderson (MS 1981) report recruitment to the silver hake populations off New England declined from a record high in 1961 to a low in 1967, then increased until 1971 and again declined to its lowest level in 1975. Recruitment for these populations continues to be at an all time low. During the USA sampling program, recruitment in the Southern New England-Middle Atlantic population was double (in numbers) that for the Gulf of Maine and Georges Bank. These recruitment estimates correlated with the difference in occurrence of silver hake cannibalism among the three areas. During this study recruitment to the Scotian Shelf silver hake population was at an all time high (Waldron *et al.*, MS 1988). The similarity between the Scotian Shelf and Southern New England-Middle Atlantic rate of cannibalism suggests that cannibalism may be density dependent (i.e. more recruitment means more cannibalism).

This analysis of silver hake diet by age group indicated a trend of consuming progressively larger prey taxa with increasing predator size. Although crustaceans (particularly *M. norvegica*) were an important component in the diet for all ages, their relative contribution by weight was far greater in smaller, younger fish (ages 1–3). Switching to fish and molluscs as prey was evident in larger silver hake (age 4+), implying selection towards larger sized prey. Swan and Clay (MS 1979) and Clay *et al.* (MS 1984) report similar results, however, the latter study indicates that crustaceans and fish comprise the bulk of the diet with little reference to molluscs. The occurrence of *I. illecebrosus* in the diet during the 1982-85 sampling period may reflect a peak in the abundance of this species and suggests that silver hake are to a certain degree opportunistic in their feeding habits.

The number of prey consumed was highly correlated to prey size. The predator's usual strategy may be to consume as much prey as possible with minimal effort. As an illustration, it may require less energy for a predator to eat large numbers of relatively slow moving, usually highly aggregated krill, than to attack a faster moving prey such as a fish.

The differences noted in diet between sexes can be interpreted as largely reflective predator-size related differences in prey selection. Because females are larger and hence faster than males, they are able to consume larger, highly mobile prey (i.e. fish and squid). Males on the other hand, tend to be smaller at age and therefore concentrate much of their feeding activity on crustaceans, which are abundant and easily obtained. There is a marked difference in the growth and weight at length between male and female silver hake. After age 4 the dichotomy in size between the sexes increases. Waldron and Fanning (MS 1986) concluded that by age 6 the majority of males were not in the population suggesting that after age 5, mortality on male silver hake was very high. The cause of such high mortality could be from a variety of factors such as cannibalism, predation or some other natural influence.

Seasonal differences in diet are most likely attributable to the availability of prey items and opportunistic predation patterns. The high cannibalism may indicate a lack of other prey as well the availability of the most recent silver hake year-classes. During this time period the silver hake population was experiencing very high recruitment (Waldron *et al.*, MS 1992).

The inter-temporal age-specific predation demonstrates a similar pattern seen for the total sample. There was a heavy dependence on crustaceans in all seasons for the younger age groups 1-3. Fish predation by these age-groups was important in the spring and summer. Predation on fish was substantial for age group 4 and older and the highest percent by weight occurred in the autumn. As stated above, since spawning occurs primarily in the August-September months, this heavier predation on fish, by older silver hake, appears closely linked to the occurrence of those juvenile silver hake.

In conclusion silver hake on the Scotian Shelf are opportunistic predators preying heavily on crustaceans and fish. There appeared to be little differences in diet composition between males and females once age was considered. There is a clear shift in the diet composition as they become older and by age 6 the diet has shifted from one dominated by invertebrates to one largely composed of fish. Overall, the diet changed from one largely composed of fish in the spring and autumn to a mixed diet of fish, crustaceans and molluscs during the summer. There are differences in the diet composition at age during the three seasons studied, however, these changes seem to reflect more the diet of younger *versus* older fish where invertebrates are preferred by ages 1 to 3 while fish are preferred by ages 4 and older. The diet of silver hake found off New England and the Scotian Shelf are similar. However, the role of other gadoids such as haddock and cod in the diet of Scotian Shelf silver hake is not as important as that assumed for the New England area. Cannibalism was observed and should play a significant role in the regulation of this species.

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