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Food and Feeding of Silver hake (*Merluccius bilinearis* Mitchill), on the Scotian Shelf with Special Reference to Cannibalism

by

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ABSTRACT

Stomach contents of 3779 hake were examined for major prey species. Cannibalism accounted for a major part of the diet of large hake (≥ 40cm), the remainder being made up of other fish and squid, smaller hake (≤ 30cm) fed almost exclusively on euphausiids and shrimp. A daily dietary intake of 4% of body weight was estimated for hake from 10 to 19 cm in length. A cannibalism-at-age predation matrix was constructed. It shows a first quantitative approximation of the potential regulatory effect hake can have on their own numbers.

INTRODUCTION

Silver hake, Merluccius bilinearis, are voracious predators with a large terminal mouth with rows of needle-like teeth well suited to seizing fleeing prey (Bigelow and Schroeder, 1953). Micheals and Bowman (1983) point out that hake have the physiological characteristics of fish eaters (ie. short gill rakers, large stomach, short intestine, pyloric caecae, etc.), this coupled with their streamlined, fusiform shape and strong swimming ability make these hake well suited for pelagic and near bottom predation. Their high levels of numerical and biomass abundance (Koeller, 1980) make them one of the major regulatory components of the Northwest Atlantic ecosystem (Bowman, 1980). Sissenwine et al. (1984) estimated that silver hake and cod (Gadus morhua) consumed 40% to 50% of all those demersal fish which are preyed upon by other demersal fish [and silver hake is the major component of this].

Extensive feeding studies with wide spatial and temporal coverage in the Northwest Atlantic have been conducted on silver hake. Generally these studies give good indications of silver hake food in the spring, summer and fall, but in most cases they state that there is little or no feeding in the winter and often their coverage is greatly reduced in the winter. Many studies have indicated the opportunistic nature of the feeding of silver hake.

This project was initiated to complement the two major studies (Bowman, 1975; Bowman and Michaels, 1982; Vinogradov, 1972, 1983), conducted in the late 1960's and early 1970's, times of relatively high abundance of hake and other commercial species. As hake is considered an opportunistic feeder, it was of interest to do a more limited comparative study of feeding on the hake in times of lower population abundance during the late 1970's.

This investigation attempts to define inter- and intra-specific feeding relationships and provide an indication of the trophic levels involved for the silver hake on the Scotian Shelf.

BACKGROUND TO FEEDING STUDIES

Bowman (1975) describes a series of studies carried out on the Scotian Shelf and Georges Bank and concluded that fish and crustaceans were the most common food items of silver hake , making up 96% by weight of the food present (Maurer, 1975). Specifically he found cannibalism upon smaller hake to account for 1% (frequency) of the diet - but over 50% by weight of all food eaten. Euphausiids were the only other important item in the diet. He found that the mean stomach volume was approximately 1 ml (1 g) and that 1/3 of the stomachs examined were empty. Everted stomachs were not collected and seem to be a problem for this type of study. Bowman (ibid) found that food habits were relatively constant from year to year but differed by area, season and sex. For the shelf area off western Nova Scotia it was found that, during the spring, more crustaceans were consumed and the mean weight per stomach was greater than during other seasons. Bowman (1980) showed the opportunistic nature of these fish with specific examples of haddock (Melanogrammus aeglefinus) and sand lance (Ammodytes americanus). Both of these prey species had years of exceptionally high recruitment and in those years the hake was recorded feeding at above normal rates on these prey.

Durbin et al. (1983) analysing this same data set developed estimates of daily consumption varying from approximately 1 to 3% of the body weight per day. Bowman (1975) recorded the food habits of males and females as being strikingly different. He found that males feed mainly on crustaceans and females on fish, and the mean weight of stomach contents for females was 4.9 g whereas it was only 0.6 g for males. No mention was made of size of fish in his study, but it is quite likely that females were larger in mean size than the males. Durbin et al. (1983) did not mention sex but did find similar results for small and large fish respectively. A study by Vinogradov (1972) shows that smaller silver hake (<21 cm) feed almost exclusively on crustaceans, and at larger lengths (>40 cm) the females feed almost exclusively on fish. Part of this difference in feeding attributed to sex is in fact related to size of fish, as females grow larger than males they would be expected to feed more heavily on fish. This latter study showed an increase in cannibalism from 1% at 20 cm to 9% at 50 cm, fish ingestion in general over the same length range changed from 10%-95% (frequency of occurrence), shrimp and euphausiids followed an opposite pattern.

Vinogradov (ibid) also found a seasonal pattern of feeding on the Scotian Shelf. Maximum feeding in most areas seemed to occur in the spring and lowest feeding in the winter. Fish from George's Bank had other fish as their most important food item and maximum feeding occurred in August. No indication of possible differences in size of fish sampled in these two areas was given.

In a study in the New York Bight area, Schaefer (1960) found that fish constituted the main portion (72% by volume) of the silver hake diet. Specifically he found that from February to May, 30% of feeding fish were cannibalizing smaller hake, whereas in January and February this level was only 1%. It was also noted that a hake can consume another fish almost half its own length. This he suggested shows the possibility that during a year where there is a shortage in the food supply, silver hake could influence its own population size.

Maurer (1975) found cannibalism to be more significant in the diet of silver hake than any of the other 28 species considered. He also reported that silver hake accounted for over 30% of the mortality to silver hake due to predation.

Another variable to consider in feeding studies is time of day. A study by Alton and Nelson (1970) showed that Pacific hake (Merluccius productus) follow their food items and thus undergo a vertical migration during the evenings and early mornings. It can be assumed feeding occurs somewhere between sunset and early morning as there was generally a marked decrease in the number of empty stomachs during this time period.

MATERIALS AND METHODS

Stomachs were collected from research vessel cruises, including government, chartered, and commercial trawlers; and from the International Observer Program sampling from commercial vessels from the U.S.S.R., Cuba, and Japan (Table 1). These 3779 stomachs were collected over the five year period 1976-1980, most were from the Scotian Shelf with some from Georges Bank. Stomachs were examined using two techniques - first, detailed laboratory analysis (included about 42% of the stomachs) and second, gross analysis on board the sampled vessel; this latter included length measurements of the predator and prey and counting the numbers of each of the major prey species. All vessels whose catches were sampled in this study used bottom type otter trawls with various small ($\leq$ 60 mm) codends. Fishing and sampling were carried out on a 24 hour basis.

Classification of prey was carried to the species level only for large prey items (such as fish and squid). The use of broad taxonomic categories such as decapods, euphasiids, etc. was required as this study was 1) conducted largely in the field by 'gross analysis', and 2) aimed towards an investigation of cannibalism and predation upon other commercial fish and squid species. The following list indicates some of the more important components of the categories used: amphipods include gammariids and hyperiids; euphausiids include a few known occurrences of mysiids; copepods include calanoids; and 'other fish' include red hake (Urophysis chuss), haddock, butterfish (Peprilus triacanthus), and various flatfish as well as undidentifiable partly digested remains.

Stomachs for laboratory analysis were removed from the fish, put into a plastic bag with formalin and labelled with date, total length, sex, and location. In some cases, the whole fish were frozen and returned to the laboratory for dissection and detailed analysis. These fish were then measured for total length and weight and the stomachs removed and placed in formalin for later analysis. It was found that placing the stomach in formalin aids analysis as it made the contents firmer; frozen stomachs were consequently 'pickled' in formalin before analysis. Stomach fullness was estimated and recorded using the following subjective guidelines: 0 = empty; 1 = empty to 1/4 full; 2 = 1/4 to 1/2 full; 3 = 1/2 to 3/4 full and 4 = 3/4 to full. Throughout this report 'sampled fish' refer to all fish collected - including ones with everted stomachs; 'feeding fish' refer to all fish with food in their stomachs and in some special cases (as mentioned in the text) it includes fish with empty (but not everted) stomachs. The preserved stomachs were opened in the laboratory, scraped out and washed clean of all contents. The stomach contents were then separated and individual food items counted using a binocular microscope. Excess liquid was drained off and the contents lightly compacted in a graduated cylinder in order to record the volume to the nearest 0.1 ml. A subsample of these volumes were converted to blotted dry weight and gave a conversion factor of 0.45 g per ml. Recorded volumes of stomachs are for all contents other than fish or squid. This was done in order to reduce the skewness in the distribution of stomach contents between the mean volume and median volume. The total or mantle length was recorded for fish or squid, respectively.

Scales were often observed in the stomach contents of hake. These were not recorded for as Davies (1949) points out, scales indicate one of three possiblities. First, the fish was actually feeding on another fish and only a few scales remain, second, they were taken in as food from the ocean bottom or water column, or third, that the scales are present due to biting at another fish and getting only a clump of scales. For single scales the second alternative is most feasible whereas when clumps of scales are found in the stomach (often the case in this study) the third possibility is most likely. The incidence of this phenomenon would be greatly increased when fish are crushed together in a trawl during capture.

The biggest difficulty in conducting a feeding study over several years with many different staff members is maintaining accuracy and consistency of data. This is particularly important in the identification of prey species. Because of this, many prey species had to be combined into large taxonomic groups to facilitate the 'gross' data analysis on board the research vessels.

Everted stomachs are a problem in any feeding study. In the case of silver hake, eversion does not seem to be directly related to depth. Davies (1949) found everted stomachs in line-caught fish from shallow waters and since there was little pressure change it is probable that eversion is due as much to stress as to pressure. If this is the case, then there is very little that can be done about this problem. Everted stomachs have not been used in calculations of feeding or frequency rates in this study.

RESULTS AND DISCUSSION OF FEEDING INVESTIGATIONS

Numbers of fish sampled indicate a skewed distribution of sex composition by length; females over 40 cm in length were commonly recorded while few males of this size were caught. Females tend to grow to a larger size than males (Hunt, 1979) and thus stratified samples will show a disproportionate number of females at these larger lengths. This tends to bias any interpretation of feeding by sex.

A curve fitted by eye was drawn for the stomach volume-degree of fullness relationship (Figure 1). The data were treated separately for fish lengths 0-19 cm and 20-40 cm. This shows that although a subjective measure, stomach fullness does give a quantitative indication without undo variation. This relationship is based on all prey items other than fish or squid. The larger fish ingest slightly more 'other (none fish) prey' than do the smaller fish - thus when the larger fishes' additional fish and squid prey are added, their dietary intake increases considerably. Using this same data (R/V Foton subset) for the 10 to 19 cm hake we calculated the daily dietary contents of the stomach. Converting the stomach volume to weight with the conversion factor of 0.45 g per ml, and using the mean weight of 35 g for fish in the 10 to 19 cm range, a daily stomach content level was found to be 4% of body weight for the months of October and November. The total diet of this size range of hake was entirely 'other prey' - and as such is comparable to the similar tables in Durbin et al. (1983). This daily stomach content level would have to be corrected to give a mean daily intake level. This correction would compensate for the time to digestion (see later discussion) which in this case we assume to be 1 day for small hake eating meals of small particle size in these warm autumn waters (mean of 8.5 C). The estimated daily intake of approximately 4% in the present study are four times higher than those of the latter work and double those of Groslein et al. (1980) and about the same as those found by Edwards and Bowman (1979). All these levels are substantially below the 8 to 10% value suggested by Vinogradov (197). There is an increase in the percentage of full and nearly full stomachs with length of fish (Tables 2, 3, and 4). Conversely, there appears to be a decrease in the percentage of nearly empty stomachs with length of fish, although this is not so clearly defined. The percentage of everted stomachs is slightly lower in larger fish. This could indicate that larger fish are less affected by either the pressure change in coming to the surface or the stress of being caught. One half to 2/3 of all examined stomachs were empty, and an additional 10% to 40%, by length groups, were everted. (Bowman(1975) found in his study that 1/3 of the stomachs examined were empty, Davies (1949) found that approximately 74% of the stomachs were found to be either empty or everted.)

Although noctural feeding patterns were observed for the silver hake in earlier work (Edwards and Bowman, 1979; Bowman and Bowman, 1980; Durbin et al., 1983), there does not appear to be any such clear relationship from this study with regard to time of day (Tables 5 and

6). There is a slight trend to decreasing percentage of full stomachs (categories 3 and 4) from midday to midnight. The heaviest feeding appears to take place between midnight and sunrise. This poor relationship is probably due to the mix of data which were combined (i.e. different months, depths and areas as well as combining all lengths) as they were too widely spread for separate diurnal time series analysis. There is an indication that the percentage of everted stomachs is highest after midnight (Table 5) corresponding to the time of peak feeding, suggesting that a recently feeding fish may be more likely to evert its stomach than one several hours after its meal. Such a relationship could lead to a downwards bias of estimates of daily feeding rates.

The percentage of fish that are multi-feeding (feeding on more than one item at a time) increases with length (Tables 7 and 8). Individual prey numbers by predator length show several distinct relationships. The average number and percentage frequency of occurrence of shrimp and euphausiids per stomach decrease with increasing predator length. The numbers of prey silver hake and other fish do not show any trend with increasing predator length, however the frequency of occurrence of this predation and cannibalism does show a very significant increase by predator length (Tables 7 and 8) This trend is true with both small prey hake and other prey fish species. Cannibalism appears to be quite common in silver hake with large hake feeding on smaller hake. The incidence of cannibalism increases from 5% with 2 year old hake to 40-100% with 6 to 10 year old hake (ages-at-length estimated from Hunt (1979 and 1980)). Similar data on frequency of occurrence and numbers of prey are presented for the fish caught in 1979 and 1980 (Table 9). All these data indicate that generally only one prey fish is consumed at a time.

Average food volume in the stomach (excluding fish and squid) increases with length of predator (Tables 7 and 8). The food volume does not include any fish or squid as the variation caused by the large prey items is extreme and implies a much larger mean stomach content than was normally observed (median value).

Reorganizing these data by depth (m), the average food volume was found to be highest (3.42 ml) in the 50 to 99 metre depths, indicating optimal feeding at less than 100 metres depth (i.e. on the banks). This obviously depends on availability of food and it can be hypothesized that <100 m is an optimal depth for crustaceans and/or small fish which make up the majority of food. Fish caught between 100 and 299 metres had food volumes between 0.35 and 0.40 ml. Large food volumes (2.5 ml) are also found between 300 and 399 metres depth, this is probably due to the larger size of hake (>40 cm) from these depths. All fish in the 400 to 599 metre depths had empty stomachs, possibly due to regurgitation when brought up from those depths.

Predator-prey size relationships are important in any consideration of age specific predation or cannibalism. There appears to be a minimum prey hake size (Figure 2) but not for 'other fish' and squid prey (Figure 3). This is probably related to the time spent by the juveniles in the pelagic zone (until approximately 10 cm in length at 3 to 5 months of age (Hunt, 1980)). Vinogradov (197) found hake fed upon other fish 20 to 50% of its own length. Schaefer (1960) found hake cannibalising smaller fish up to half their own length.

The stomach contents by predator length (cm) and month (Tables 10 and 11) do not show clear seasonal relationships. This may be due to the fact that all months are not represented and several of the months with specimens have only small samples. It appears that during the spring and early summer, euphausiids play an important role in the food of fish <40 cm, and that small prey fish and squid become increasingly more important in the latter part of the year (October to December) (Figure 4). Larger hake (>40 cm) feed mainly on squid in the late summer and early fall and increasingly on fish from October to December, although crustaceans are significant in their food throughout the year (Figure 5). Squid were commonly found in the stomachs of larger silver hake and may have had higher levels of occurrence than normal due to the high levels of squid abundance on the Scotian Shelf in the late 1970's (Rowell and Young, 1984). The seasonal pattern of squid appearance in the diet is closely related to the movement of squid into and out of the silver hake grounds, peaking in the early fall (Figure 5). Amphipods, although occasionally found in the stomachs examined, do not seem to be important in the food of hake and as Davies (1949) points out they are probably present in the stomach only due to chance.

The food web which Hickling (1935) drew up for the European hake (Merluccius vulgaris) is shown here in modified form. Davies (1949) modified this for the Cape hake (Merluccius capensis), and it is further enhanced here for silver hake (Merluccius bilinearis) (after Swan and Clay, 1979) on the east coast of North America (Figure 2). Data are not yet sufficient to indicate dietary preference of the hake, therefore, due to the opportunistic nature of it's feeding habits, it is not possible to estimate relative importance of the individual components (except in one instant in time). Vinogradov (1983) has attempted a first approximation of a relative-importance food web for the hake.

From past data reviewed and the diverse species found to be present in the stomachs of hake during this study, it can be generalised that young silver hake feed mainly on crustaceans and small fish, increasing dietary intake of fish and squid as they grow. Hake appear to be voracious and opportunistic, feeding on whatever is present in the water column at the time.

AN ATTEMPT TO QUANTIFY CANNIBALISM IN THE HAKE

Predation, and its special case cannibalism, are accepted contributors to natural mortality in general and pre-recruit mortality in particular (Sissenwine, 1984). Maurer (1975) found cannibalism to be more important in hake than in 28 other species investigated, thus it is a prime species on which to study the effects of age specific mortality applied to current fisheries management models. Cloudsley-Thompson (1959) suggested cannibalism was an important means of maintaining protein within a species and a population. The study of such intra-specific predation, while considerablely easier (in a computational sense) than inter-specific predation, should indicate some of the major cause-effect relationships involved in using age specific variable mortality estimates. One major constraint in running virtual population analysis simulations (VPA) on commercial stocks is the common need to choose one level of natural mortality for all seasons and all age classes. A means to achieve an understanding of how a portion of this mortality is distributed by age is by the construction of a matrix of age specific cannibalism by numbers. Such a matrix follows:-

		PREDATOR age									
PREY		1	2	3	4	5	6	7	8	9	10
age	1	0	1.5	2.5	2.5	13	13	13	15	0	0
	2	0	0	0	2.0	16	21	21	23	69	0
	3	0	0	0	0	7	11	15	18	49	49

where an approximation to the number of prey-at-age eaten by each predator-at-age was derived as follows:-

N-at-age = HE x Feed x (Season x 365) x Space / Evacuation

where:- N-at-age is the number of prey-at-age eaten by a predator-at-age per annum;

HE is the number of hake (of prey age) found in the stomach of another hake (of predator age). These values are found from Tables 7, 8, and 9.

Feed is the percent frequency of occurrence of HE. These values are found from Tables 7, 8, and 9.

Season is the percentage of the year of hake feeding at the above rates. For this work we are assuming a knife edge feeding pattern with no feeding in the winter and spring/summer/autumn represented by our data. This is probably a reasonable approximation as the majority of our samples were collected in the spring and summer, times of high feeding rates, which would bias upwards any mean feeding levels.

Space is the percentage of geographic overlap of predator and prey at age. For age 1 prey this was assumed to be 50% as they are in a pelagic phase for 3 to 6 months and so are free from cannibalism (although not free from predation in general). For ages 2+ we have assumed 100% until data become available to indicate otherwise.

Evacuation is the speed in days of digestion of a meal of prey-at-age size by a predator-at-age. Durbin et al. (1983) provide a summary of gastric evacuation rates for hake and other fish. Factors found to affect this rate include temperature, food (particle) size, meal size (stomach fullness), food type, activity and stress. In our present case, as we are only investigating cannibalism, the problem is greatly simplified. We can assume that all fish (predators) feeding on smaller hake will have a large meal (ie. a full stomach). Fish have been observed to digest prey fish more slowly than other (smaller) prey types (Durbin et al., 1983), this may be due to either the larger particle size of the meal or the fish flesh itself being less digestible [unlikely]. Tyler (1970) found the time of evacuation of small invertebrate pieces varied from approximately 24 hours at 10 to 15 C to 48 hours at 2 C. MacDonald et al. (1982) found rates for similar prey types at 5 to 10 C to be approximately 24 hours for four different marine fish species. Thus any estimate for evacuation rates of cannibalised hake at an average of 6 to 10 C would be in the order of 2 to 4 days per meal of larger prey and 1 to 2 days per meal of smaller prey, dependent on the temperature. Our approximation for this is 1.5 days for a prey-at-age 1, 2.5 days for a prey-at-age 2, and 3.5 days for a prey-at-age 3.

These values, put forward as first approximations, require further study and refinement. They do, however, point out the great differences that are present in age specific natural mortality. Such heavy cannibalism of the older year classes (6+) on the younger fish (1 and 2 year olds in particular) would result in a lower than expected MSY with an unfished stock; and a stock with a fast recovery rate when overfished, especially in the older age groups. Cannibalism is potentially very important in regulation of some major fish stocks, ie. silver hake - up to 30% by weight (Schaefer, 1960), cod - up to 20% by weight (Daan, 1973), squid - up to 15% by weight (Froerman, 1983).

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REFERENCES

Alton, M.S. and Nelson, M.O. (1970) Food of the Pacific hake, Merluccius productus, in Washington and northern Oregon coastal waters. Circ. U.S. Fish & Wild. Serv. 332:35-42

Best, E.A. (1963). Contribution to the biology of the Pacific Hake, Merluccius productus (Ayres). Calif.Coop.OceanicFish.Invest. Rep 9: 51-56

Bigelow,H.B. and W.C. Schroeder (1953) Fishes of the Gulf of Maine. U.S. Fish and Wildlife Serv., Fish.Bull. 74.

Bowman, R.E. (1975) Food habits of Atlantic cod, haddock, and silver hake in the Northwest Atlantic, 1969-1972. In: Food Chain Investigations, Food Habits of Marine Fishes of the Nortwest Atlantic. Data Report. US Dept. Comm. NOAA pp 1-53.

Bowman, R.E. (1980) Silver hake's (Merluccius bilinearis) regulatory influence on fishes of the Northwest Atlantic. N.M.F.S., Woods Hole Laboratory, Lab. Ref. Doc. 80-05.

Bowman, R.E. (1980) Food of silver hake (Merluccius bilinearis). US NMFS, Woods Hole Laboratory, Lab. Ref. Doc. 80-31.

Bowman, R.E. and E.W. Bowman (1980) Diurnal variation in the feeding and catchability of silver hake Merluccius bilinearis. Can.J.Fish. Aquat.Sci.37:1565-1572.

Bowman, R.E., R.O. Maurer and J.A. Murphy (1976) Stomach contents of twenty nine fish species from five regions in the Northwest Atlantic. Data Report. US NMFS, Woods Hole Laboratory, Lab. Ref. Doc. 76-10.

Bowman, R.E. and W.L. Michaels (1982) Food of seventeen species of Northwest Atlantic fish: Part I. Examination by predator length and geographic area. N.M.F.S., Woods Hole Laboratory, Lab.Ref. No. 82-16.

Cloudsley-Thompson (1959) The significance of cannibalism. New Scientist, 5(130):1068-1070.

Daan, N. (1973) A quantitative analysis of food intake of North Sea cod Gadus morhua. Netherlands J.Sea Res.6(4):479-517.

Davies, D.H. (1949) Preliminary investigations on the foods of South African fishes with notes on the general fauna of the area. Fish Mar. Biol. Survey Div., Union S.A., Invest. Rep. No 11 pp 36.

Durbin, E.G., A.G. Durbin, R.W. Langton and R.E. Bowman (1983) Stomach contents of silver hake, Merluccius bilinearis, and Atlantic cod, Gadus morhua, and estimates of their daily rations. Fish.Bull.,US.81(3):437-454.

Edwards, R.L. and R.E. Bowman (1979) Food consumed by continental shelf fishes. In: Predator-prey systems in fisheries management (H. Clepper - editor). Sport Fish.Inst.,Washington, U.S.A. pp387-406.

Froerman, Yu.M. (1983) Feeding spectrum and food relationships of short fin squid (Illex illecebrosus Leseaur, 1821). NAFO SCR Doc 83/IX/82.

Grosslein, M.D., R.W. Langton and M.P. Sissenwine (1980) Recent fluctuations in pelagic fish stocks of the Northwest Atlantic, Georges Bank region, in relation to species interactions. Rapp.P.-V. Reun.Cons.Int.Explor.Mer. 177:374-404.

Hickling, C.F. (1935) The hake and the hake fishery. The Buckley Lectures. London, pp 142.

Hunt, J.J. (1979) Back-calculation of length-at-age from otoliths for silver hake of the Scotian Shelf. ICNAF Sel. Pap.5:11-18.

Hunt, J.J. (1980) Guidelines for age determination of silver hake, Merluccius bilinearis, using otoliths. J.Northw.Atl.Fish.Sci. 1:65-80.

Koeller, P.A. (1980) Biomass estimates from Canadian research vessel surveys on the Scotian Shelf and in the Gulf of St. Lawrence from 1970 to 1979. CAFSAC Res.Doc. 80/18.

Langton, R.W. and R.E. Bowman (1980) Food of fifteen Northwest Atlantic gadiform fishes. US. Dept.Comm., NOAA Tech.Rept. SSRF-740.

MacDonald, J.S., K.G.Waiwood and R.H. Green (1982) Rates of digestion of different prey in Atlantic cod (Gadus morhua), ocean pout (Macrozoarces americanus), winter flounder (Pseudopleuronectis americanus), and American plaice (Hippoglossoides platessoides). Can.J.Fish.Aquat.Sci. 39:651-659.

Maurer, R. (1975) A preliminary descrition of some important feeding relationships. ICNAF Res. Doc. 75/IX/130.

Michaels, W.L. and R.E. Bowman (1983) Food of seventeen species of Northwest Atlantic fish: Part II. Examination by year and listing of prey species. N.M.F.S., Woods Hole Laboratory, Lab.Ref. No. 82-17.

Sissenwine, M.P., E.B. Cohen and M.D. Grosslein (1984) Structure of the Georges Bank ecosysytem. Rapp.P.-v.Reun.Cons.Int.Explor.Mer. 183:243-254.

Schaefer, R.H. (1960) Growth and feeding habits of the whiting or silver hake in the New York Bight. N.Y. Fish & Game J. (2):85-98.

Swan, B.K. and D. Clay (1979) Feeding study on silver hake (Merluccius bilinearis) taken from the Scotian Shelf and ICNAF Subarea 5. ICNAF Res.Doc.79/VI/49.

Tyler, A.V. (1970) Rates of gastric emptying in young cod. J.Fish.Res.Bd. 27:1177-1189.

Vinogradov, V.I. (1972) Studies of the food habits of silver and red hake in the Northwest Atlantic area, 1965-67. ICNAF Res. Bull. 9:41-50.

Vinogradov, V. I.]977. Daily feeding rhythms and food rations of the silver hake, Merluccius bilinearis, and the red hake (Urophysis chuss), in the Northwest Atlantic. J. Ichthyology, 17(4): 600-610.

Vinogradov, V.I. (1983) Food relationships between silver hake and red hake and other fish species on Georges Bank and in adjacent waters. NAFO SCR Doc. 83/IX/80.

Table 1. Location, date and number of silver hake stomachs analysed from each sampling source during the time of this feeding study.

Cruise/Program	Date	Location	Number of stomachs	Type of analysis
1.M/V Cape Argos	Oct/Dec 76	NAFO Div 4&5	885	laboratory
2.R/V Foton	Oct/Nov 77	Emerald Bank Emerald Basin	411	laboratory
3.R/V Prince	April 78	Emerald Bank Emerald Basin	43	laboratory
4.Cuban commercial trawler	June 78	Sable Island Bank Emerald Bank	106	laboratory
5.R/V Lady Hammond LH006	Oct/Nov 78	NAFO Sub-div.4W	148	laboratory
6.R/V Lady Hammond LH006	Oct/Nov 78	NAFO Sub-div.4W	44	gross
7.Japanese commercial trawler	Oct/Dec 78	NAFO Sub-div.4W	74	gross
8.International Observer Prgm.	May/Dec 79	NAFO Sub-div. 4VW	1230	gross
9.International Observer Prgm.	May/Oct 80	NAFO Sub-div. 4VW	838	gross
	1976 - 1980	Scotian Shelf	3779	

Table 2. Numbers of silver hake by length (cm) and by sex having various levels of stomach fullness (see text). The lower half of the table indicates the percent of fish (not including those with everted stomachs) having the same levels of stomach fullness. All fish were analysed in the laboratory and were from cruises other than the R/V Foton (cruises 1,3,4,and 5 from Table 1).

FISH LENGTH	SEX	SAMPLED FISH	EVERTED STOMACHS	EMPTY	--------STOMACH FULLNESS--------- 0-25%	25-50%	50-75%	75-100%
10 - 19	MALE	21	4	12	2	2	0	1
	FEMALE	32	12	12	5	2	0	1
	COMBINED	53	16	24	7	4	0	2
20 - 29	M	261	55	97	70	24	8	7
	F	308	69	126	73	31	5	4
	C	569	124	223	143	55	13	11
30 - 39	M	126	19	45	47	8	3	4
	F	302	68	108	72	34	11	9
	C	428	87	153	119	42	14	13
40 - 49	M	5	1	2	0	0	1	1
	F	74	6	31	20	9	3	5
	C	79	7	33	20	9	4	6
50+	M	0	0	0	0	0	0	0
	F	33	3	11	4	8	3	4
	C	33	3	11	4	8	3	4

FISH LENGTH	SEX	FEEDING FISH	% EVERTED	EMPTY	--------% STOMACH FULLNESS------- 0-25%	25-50%	50-75%	75-100%
10 - 19	C	37	29	65	19	11	0	5
20 - 29	C	445	19	50	32	12	3	3
30 - 39	C	341	19	45	35	12	4	4
40 - 49	C	72	8	46	28	13	6	8
50+	C	30	8	37	13	27	10	13

Table 3. Numbers of silver hake by length (cm) and by sex having various levels of stomach fullness (see text). The lower half of the table indicates the percent of fish (not including those with everted stomachs) having the same levels of stomach fullness. All fish were analysed in the laboratory and were from the cruise of the R/V Foton in October-November 1977.

FISH LENGTH	SEX	SAMPLED FISH	EVERTED STOMACHS	STOMACH FULLNESS EMPTY	0-25%	25-50%	50-75%	75-100%
10 - 19	MALE	73	22	25	7	4	5	10
	FEMALE	89	29	32	8	10	5	5
	COMBINED	281	53	91	49	29	29	30
20 - 29	M	21	9	8	2	1	1	0
	F	7	3	4	0	0	0	0
	C	29	12	12	3	1	1	0
30 - 39	M	11	5	6	0	0	0	0
	F	24	12	4	4	1	0	3
	C	35	17	10	4	1	0	3
40 - 49	M	0	0	0	0	0	0	0
	F	6	1	3	1	0	1	0
	C	6	1	3	1	0	1	0
50+	M	0	0	0	0	0	0	0
	F	61	1	10	2	10	4	34
	C	61	1	10	2	10	4	34

FISH LENGTH	SEX	FEEDING FISH	% EVERTED	% STOMACH FULLNESS EMPTY	0-25%	25-50%	50-75%	75-100%
10 - 19	C	228	19	40	22	13	13	13
20 - 29	C	17	41	71	18	6	6	0
30 - 39	C	18	49	56	22	6	0	17
40 - 49	C	5	20	60	20	0	20	0
50+	C	60	2	17	3	17	7	57

Table 4. Numbers of silver hake by length (cm) and by sex having various levels of stomach fullness (see text). The lower half of the table indicates the percent of fish (not including those with everted stomachs) having the same levels of stomach fullness. All fish were analysed by gross analysis on board fishing vessels (cruises 6,7,8, and 9 from Table 1).

FISH LENGTH	SEX	SAMPLED FISH	EVERTED STOMACHS	--------STOMACH FULLNESS---------				
				EMPTY	0-25%	25-50%	50-75%	75-100%
10 - 19	MALE	4	0	0	0	1	2	1
	FEMALE	2	0	0	0	0	2	0
	COMBINED	11	0	1	4	1	4	1
20 - 29	M	307	18	181	54	23	11	20
	F	179	17	72	34	18	11	27
	C	487	35	253	88	42	22	47
30 - 39	M	472	27	369	43	16	6	10
	F	941	53	620	133	54	40	41
	C	1413	80	989	177	70	46	51
40 - 49	M	8	0	4	2	2	0	0
	F	156	4	100	13	10	7	22
	C	154	4	104	15	12	7	22
50+	M	0	0	0	0	0	0	0
	F	45	2	23	6	4	3	7
	C	45	2	23	6	4	3	7

FISH LENGTH	SEX	FEEDING FISH	% EVERTED	--------% STOMACH FULLNESS-------				
				EMPTY	0-25%	25-50%	50-75%	75-100%
10 - 19	C	10	0	10	40	10	40	10
20 - 29	C	447	7	56	19	9	5	11
30 - 39	C	1320	6	74	13	5	3	4
40 - 49	C	146	1	70	10	1	4	14
50+	C	37	5	57	13	8	3	19

Table 5. Numbers of silver hake (sexes and lengths combined) by time of day having various levels of stomach fullness. The lower half of the table indicates the percent of fish (not including those with everted stomachs) having the same levels of stomach fullness. All fish were analysed in the laboratory and were from cruises other than the R/V Foton (cruises 1,3,4,and 5 from Table 1).

HOUR OF DAY	SAMPLED FISH	EVERTED STOMACHS	EMPTY	0-25%	25-50%	50-75%	75-100%
			STOMACH FULLNESS				
00:00-04:59	282	70	115	61	26	1	9
05:00-07:59	170	35	80	33	9	4	9
08:00-10:59	35	10	8	14	2	0	1
11:00-13:59	183	40	80	40	15	6	2
14:00-17:59	147	23	59	45	15	5	0
18:00-20:59	108	19	50	34	3	0	2
21:00-23:59	112	17	53	30	8	1	3

HOUR OF DAY	FEEDING FISH	% EVERTED	EMPTY	0-25%	25-50%	50-75%	75-100%
			% STOMACH FULLNESS				
00:00-04:59	212	25	54	28	12	1	4
05:00-07:59	135	21	59	24	7	3	7
08:00-10:59	25	29	32	56	8	0	4
11:00-13:59	143	22	56	28	11	4	1
14:00-17:59	124	16	48	36	12	4	0
18:00-20:59	89	18	56	38	4	0	2
21:00-23:59	95	15	56	32	8	1	3

Table 6. Numbers of silver hake (sexes and lengths combined) by time of day having various levels of stomach fullness. The lower half of the table indicates the percent of fish (not including those with everted stomachs) having the same levels of stomach fullness. All fish were analysed by gross analysis on board fishing vessels (cruises 6,7,8,and 9 from Table 1).

HOUR OF DAY	SAMPLED FISH	EVERTED STOMACHS	--------STOMACH FULLNESS--------- EMPTY	0-25%	25-50%	50-75%	75-100%
00:00-04:59	307	5	227	30	18	8	19
05:00-07:59	257	15	177	29	9	5	22
08:00-10:59	227	15	150	33	12	7	10
11:00-13:59	405	16	219	46	41	12	11
14:00-17:59	574	47	357	68	28	28	46
18:00-20:59	275	12	190	49	8	6	10
21:00-23:59	79	5	67	5	2	0	0
HOUR OF DAY	**FEEDING FISH**	**% EVERTED**	**-------% STOMACH FULLNESS------- EMPTY**	**0-25%**	**25-50%**	**50-75%**	**75-100%**
00:00-04:59	302	2	75	10	6	3	6
05:00-07:59	242	6	73	12	4	2	9
08:00-10:59	212	7	71	16	6	3	5
11:00-13:59	389	4	56	12	10	3	3
14:00-17:59	527	8	68	13	5	5	9
18:00-20:59	263	4	72	19	3	2	4
21:00-23:59	74	6	91	7	3	0	0

Table 7. Mean numbers by length (cm) of prey by taxonomic groups found in a silver hake stomach. The percent frequency occurrence of feeding on that prey species is found in the lower half of the table. The average food volume (ml) does not include fish or squid (see text). These data are from feeding fish (ie. fish with stomach contents) sampled from all cruises except the R/V Foton and were analysed in the laboratory (cruises 1,3,4,and 5 from Table 1).

FISH LENGTH	FEEDING FISH	FOOD VOLUME	# MULTI FEEDING	EUPHAUSIIDS	DECAPODS	AMPHIPODS	COPEPODS	SILVER HAKE	OTHER FISH
10-19	9	0.74 ± 1.95	1	0	16.56 ± 18.58	2.0 ± 0.0	0	0	0
20-29	143	0.54 ± 1.36	25	10.48 ± 21.80	5.48 ± 8.88	1.77 ± 1.54	1.67 ± 0.98	1.25 ± 0.71	1.00 ± 0.00
30-39	152	1.10 ± 2.81	29	11.12 ± 14.71	6.33 ± 9.76	7.13 ± 15.1	4.50 ± 6.74	1.00 ± 0.00	1.24 ± 0.56
40-49	30	3.38 ± 8.71	8	12.33 ± 19.63	1.79 ± 1.19	1.50 ± 0.71	0	1.00 ± 0.00	1.23 ± 0.60
50+	14	13.31 ± 30.67	4	1.00 ± 0.00	1.50 ± 0.71	0	1.00 ± 0.00	1.00 ± 0.00	1.14 ± 0.38
			%	-----------%	FREQUENCY	OF	OCCURRENCE------------------		
10-19	9		11	0	100	11	0	0	0
20-29	143		18	36	56	8	8	6	7
30-39	152		19	22	71	5	6	5	11
40-49	30		27	10	47	7	0	20	43
50+	14		29	21	14	0	7	36	50

Table 8. Mean numbers by length (cm) of prey by taxonomic group found in a silver hake stomach. The percent frequency occurrence of feeding on that prey species is found in the lower half of the table. The average food volume (ml) does not include fish or squid (see text). These data are from feeding fish (ie. fish with stomach contents) sampled from the R/V Foton in October-November 1977 and were analysed in the laboratory.

FISH LENGTH	FEEDING FISH	FOOD VOLUME	# MULTI FEEDING	EUPHAUSIIDS	DECAPODS	AMPHIPODS	COPEPODS	SILVER HAKE	OTHER FISH
10-19	177	0.9±1.24	21	18.4±22.9	1.0±0.0	2.4±1.1	3.0±2.8	0	0
20-29	10	0.7±0.7	1	21.2±29.8	0	0	0	0	0
30-39	12	1.1±1.1	4	3.3±3.6	1.0±0.0	1.6±1.4	0	1.0±0.0	1.5±0.5
40-49	3	4.1	0	2	0	0	0	1.0±0.0	1.0
50+	50	0	0	0	0	0	0	1.5±1.1	1.0±0.0
			%	---------%	FREQUENCY	OF	OCCURRENCE------	-------	
10-19	177	0	18	92	6	7	2	0	0
20-29	10	0	10	50	0	0	0	0	0
30-39	12	0	33	50	17	25	0	17	17
40-49	3	0	0	33	0	0	0	66	33
50+	50	0	44	0	0	0	0	100	44

Table 9. Mean numbers by length (cm) of prey by taxonomic group found in a silver hake stomach. The percent frequency occurrence of feeding on that prey species is found in the lower half of the table. The average food volume (ml) does not include fish or squid (see text). These data are from feeding fish (ie. fish with stomach contents) processed at sea by gross analysis (cruises 6,7,8, and 9 from Table 1).

FISH LENGTH	FEEDING FISH	# MULTI FEEDING	EUPHAUSIIDS	DECAPODS	SQUID	SILVER HAKE	OTHER FISH	UNIDENT.
10-19	11	0	12.5±10.3	0	0	0	0	-
20-29	227	5	21.9±22.7	3.0±5.3	1.0±0.0	1.0±0.0	1.0±0.0	-
30-39	320	19	17.3±22.4	2.8±3.6	1.1±0.3	1.0±0.0	1.9±1.8	-
40-49	60	7	8.5±6.4	1.5±0.7	1.2±0.5	1.0±0.0	1.0±0.0	-
50+	18	1	0	0	1.3±0.6	1.0±0.0	1.0±0.0	-
			%	---------%	FREQUENCY	OF	OCCURRENCE	-------------
10-19	11	0	82	9	9	0	0	0
20-29	227	2	76	7	1	1	4	13
30-39	320	6	58	9	14	3	9	13
40-49	60	12	3	3	60	17	10	18
50+	18	6	0	0	56	22	17	17

Table 10. Number of silver hake by length (cm) and by month feeding on various prey by taxonomic group. The percent frequency occurrence of feeding on that prey species is found in the lower half of the table. These data are from feeding fish (ie. fish with stomach contents) sampled from all cruises except the R/V Foton and were analysed in the laboratory (cruises 1,3,4,and 5 from Table 1).

FISH LENGTH	MONTH	FEEDING FISH	EUPHAUSIID	DECAPODS	AMPHIPODS	CYCLOPODS	SQUID	MOLLUSCS	SILVER HAKE	OTHER FISH
10-39	4	3	0	2	0	1	0	0	0	0
40+	4	0	0	0	0	0	0	0	0	0
10-39	6	40	0	40	2	1	0	0	0	0
40+	6	0	0	0	0	0	0	0	0	0
10-39	10	66	5	51	1	3	2	2	0	10
40+	10	8	0	0	0	0	2	0	3	3
10-39	11	153	71	89	5	5	6	0	15	10
40+	11	35	6	15	2	1	1	0	8	14
10-39	12	49	9	16	15	11	1	0	0	6
40+	12	4	0	1	0	0	0	0	0	3
			---------------%	FREQUENCY	OF	OCCURRENCE	-----------------			
10-39	4	3	0	67	0	33	0	0	0	0
40+	4	0	0	0	0	0	0	0	0	0
10-39	6	40	0	100	5	3	0	0	0	0
40+	6	0	0	0	0	0	0	0	0	0
10-39	10	66	8	77	2	5	3	3	0	15
40+	10	8	0	0	0	0	25	0	38	38
10-39	11	153	46	58	3	3	4	0	10	7
40+	11	35	17	43	6	3	3	0	23	40
10-39	12	49	18	33	30	22	2	0	0	12
40+	12	4	0	25	0	0	0	0	0	75

Table 11. Number of silver hake by length (cm) by month feeding on various prey by taxonomic group. The percent frequency occurrence of feeding on that prey species is found in the lower half of the table. These data were from feeding fish (ie. fish with stomach contents) processed at sea by gross analysis (cruises 6,7,8, and 9 from Table 1).

FISH LENGTH	MONTH	FEEDING FISH	EUPHAUSIIDS	DECAPODS	SILVER HAKE	OTHER FISH	SQUID
10-39	5	41	39	2	0	0	3
40+	5	0	0	0	0	0	0
10-39	6	125	94	11	2	3	13
40+	6	14	2	1	4	1	10
10-39	7	127	48	21	2	8	22
40+	7	30	0	5	6	1	13
10-39	8	66	26	21	1	6	15
40+	8	5	1	1	1	0	5
10-39	9	135	64	27	0	3	2
40+	9	19	2	0	6	1	13
10-39	10	16	7	10	0	1	0
40+	10	9	0	3	3	2	3
10-39	11	8	0	5	2	1	0
40+	11	4	0	0	1	1	1
10-39	12	4	0	4	0	0	0
40+	12	0	0	0	0	0	0
			---%	FREQUENCY	OF	OCCURRENCE----	
10-39	5	41	97	5	0	0	8
40+	5	0	0	0	0	0	0
10-39	6	125	82	9	2	2	9
40+	6	14	0	7	29	7	71
10-39	7	127	38	19	2	6	18
40+	7	30	0	17	20	3	43
10-39	8	66	41	47	2	9	23
40+	8	5	0	20	20	0	100
10-39	9	135	50	20	0	2	1
40+	9	19	5	0	32	5	74
10-39	10	16	58	83	0	8	8
40+	10	9	0	37	25	25	37
10-39	11	8	0	63	25	13	0
40+	11	4	0	0	25	25	25
10-39	12	4	0	100	0	0	0
40+	12	0	0	0	0	0	0

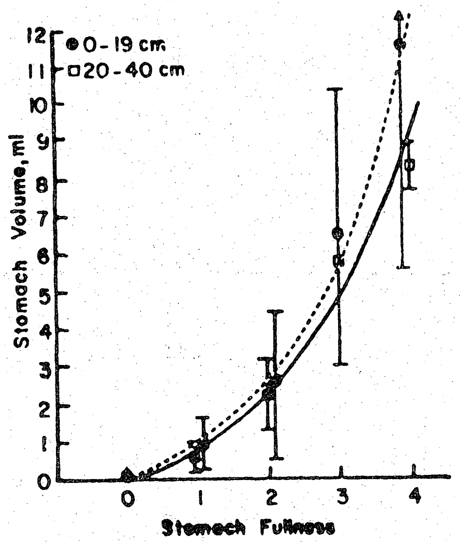

Figure 1. Relationship between stomach volume and stomach fullness for two length groups of fish, 10 to 19 cm and 20 to 39 cm Stomach fullness is a subjective measure of the amount of food present where 0 = empty, 1 = 0 to 25% full, 2 = 26 to 50% full, 3 = 51 to 75%, 4 = 76 to 100% full.

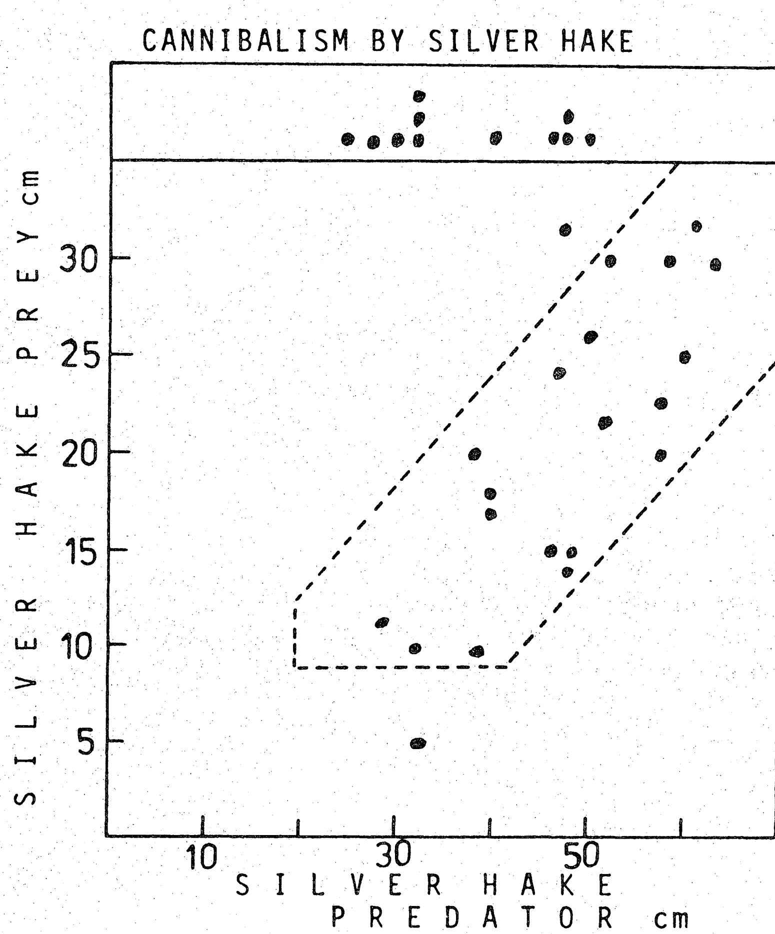

Figure 2. Predator-prey size relationship for cannibalised hake. The rectangular box at the top indicates the size of predator for which an unmeasured hake was observed in the stomach.

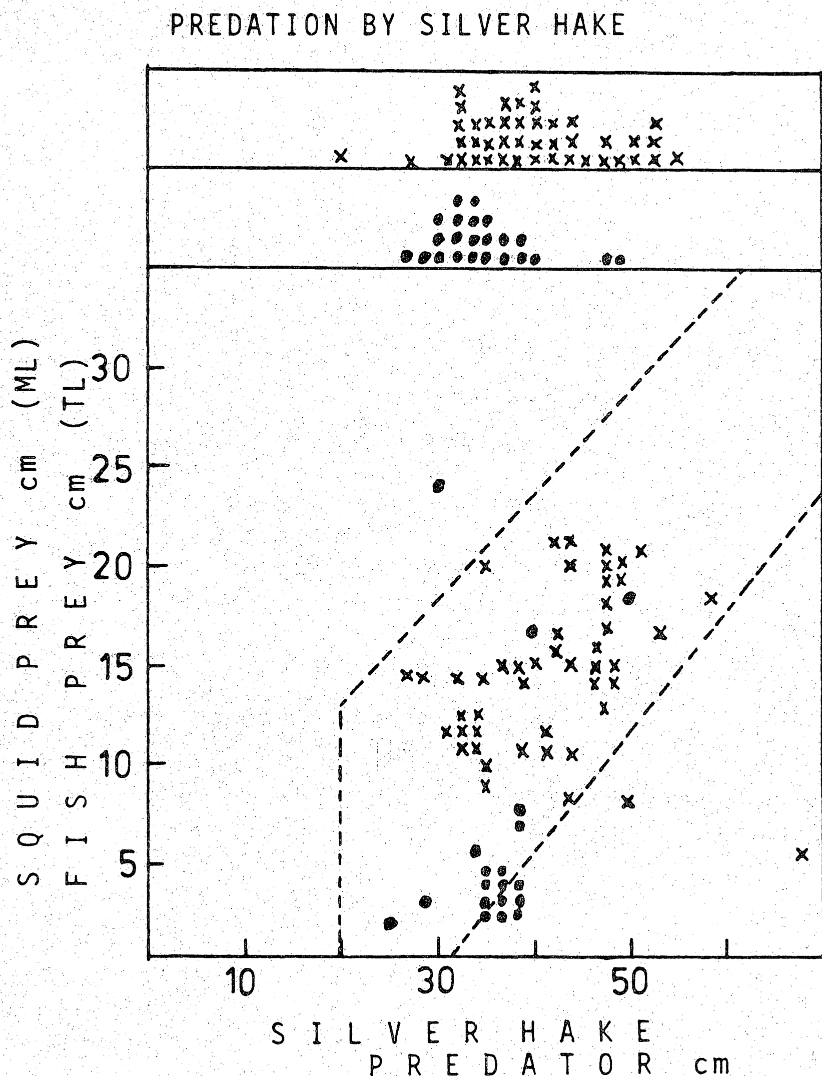

Figure 3. Predator-prey size relationship for predation upon other fish (none silver hake) "o" and squid "x". The rectangular boxes at the top indicate the size of predator for which an unmeasured prey was observed in the stomach.

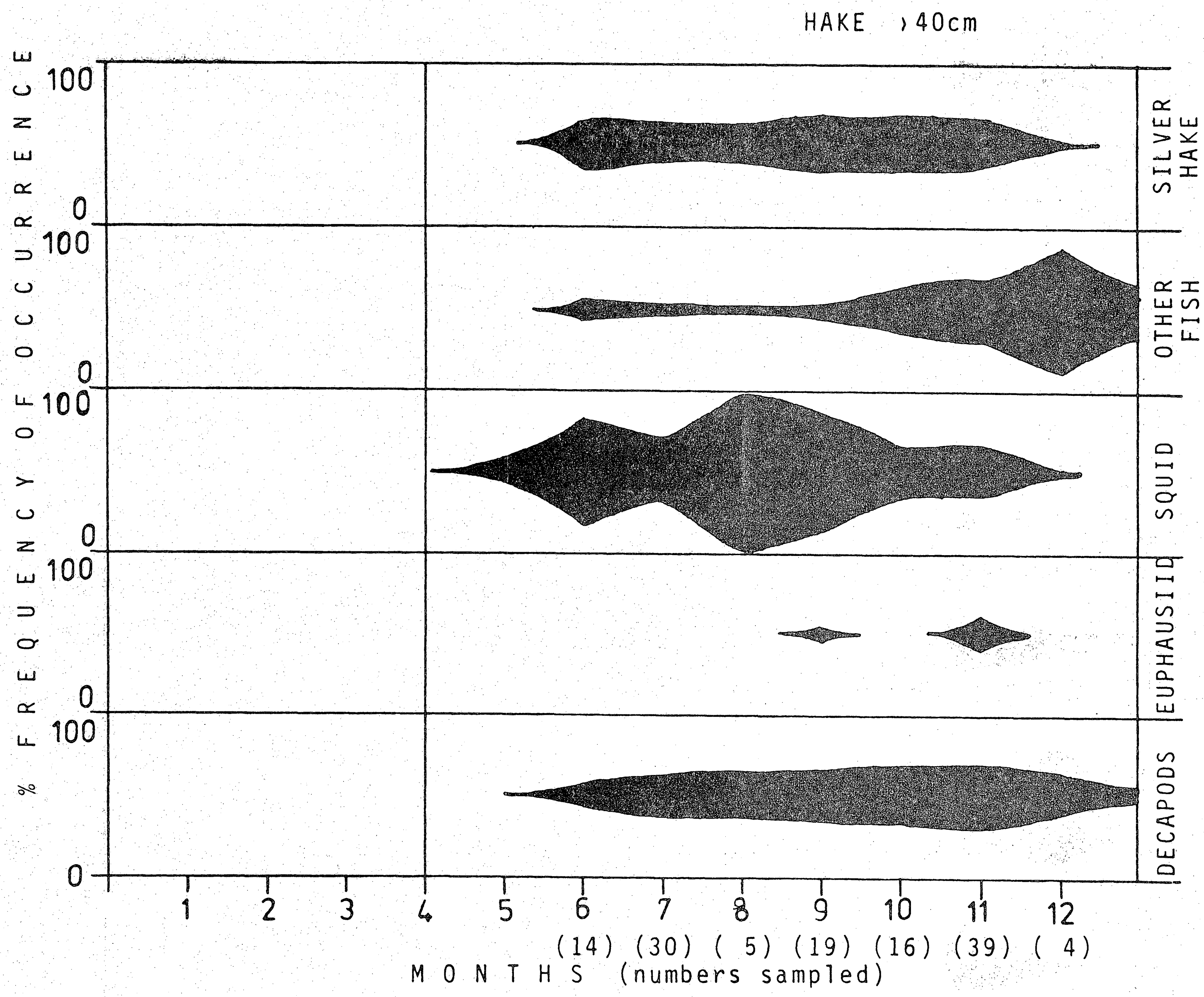

Figure 4. Percent frequency of occurrence of feeding on various prey by month for silver hake less than 40 cm. Numbers in brackets indicate the number of fish included in that months sample.

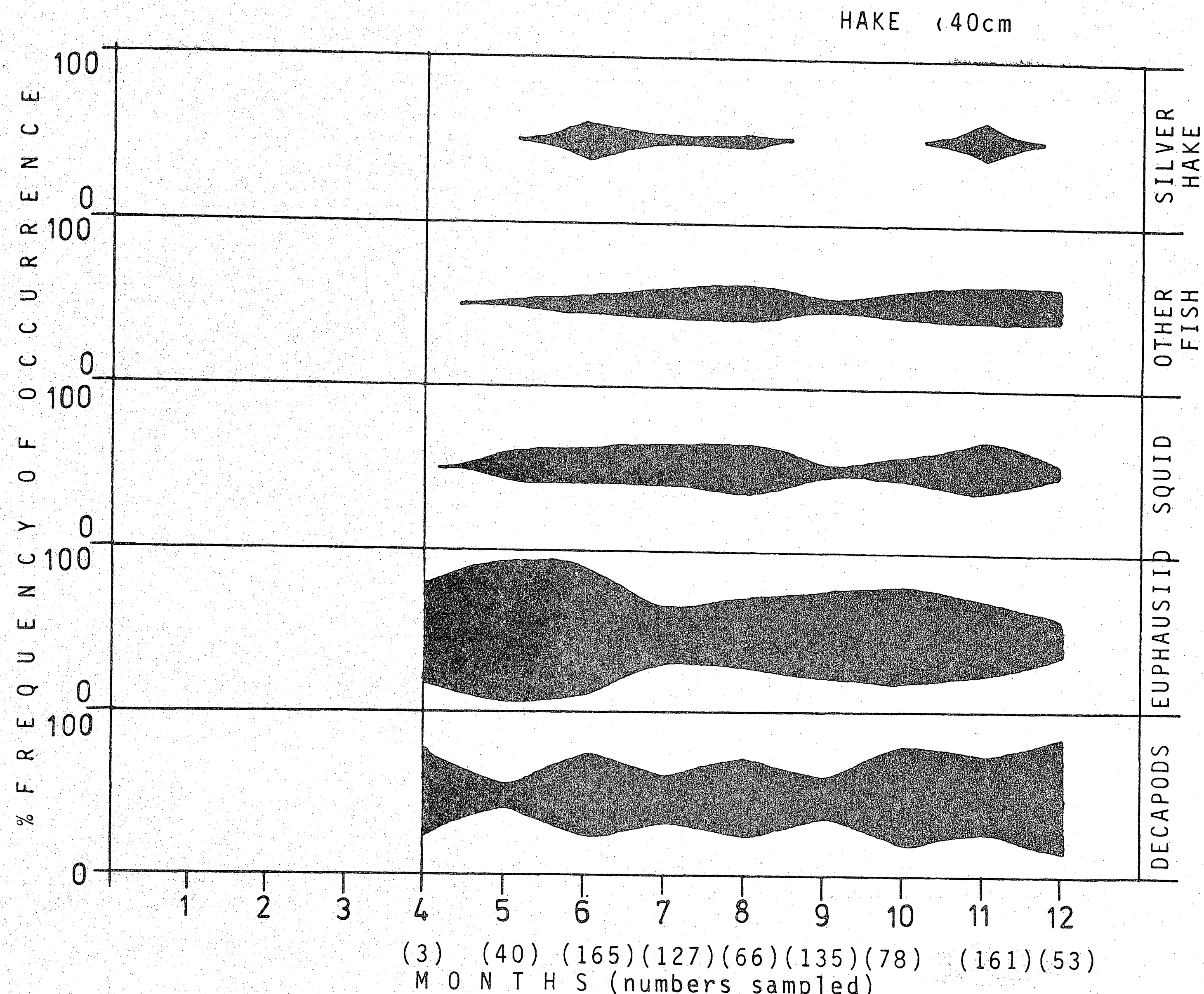

Figure 5. Percent frequency of occurrence of feeding on various prey by month for silver hake more than 40 cm. Numbers in brackets indicate the number of fish included in that months sample.

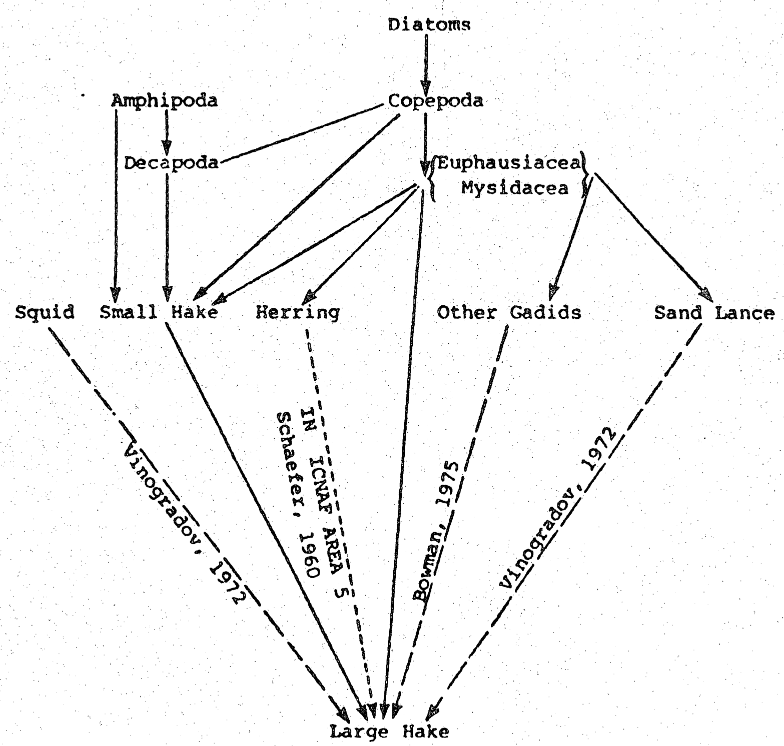

Figure 6. A modified food web for silver hake from the Scotian Shelf and Georges Bank area (modified after Hickling, 1935).