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Cannibalism in the Scotian Shelf Silver Hake Population
and How it May Influence Population Status

by

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Abstract

The Scotian Shelf silver hake population has varied considerably over the last 30 and in particular the last 20 years. The diet of silver hake is primarily small crustaceans, however, larger members of the population show an increasing rates of cannibalism. An age structured sequential population model to investigate the impact of cannibalism on the silver hake population was constructed using empirical data on diet preference, estimated consumption rates and previous assumptions of natural mortality. Cannibalism mortality was then observed to exceed both fishing and residual natural mortalities. In particular, the presence of large year classes had a dampening effect on subsequent recruiting year classes. Cannibalism also influences estimates of fishing mortalities at age which has a direct impact on estimates of yield per recruit and the estimated $F_{0.1}$. This does have a marginal influence on the subsequent projections for this stock.

Introduction

Silver hake (*Merluccius bilinearis*) is one of the largest finfish resources on the Scotian Shelf. The fishery for this species began in 1962 and flourishes to the present day. Throughout the history of this fishery catches have fluctuated between 60,000 and 300,000 tons. The pattern is repetitive with some 10-13 years between each peak. Biomass estimates also reflect this pattern and are closely linked to fluctuations in other Scotian Shelf finfish species.

The fluctuations in the population biomass of silver hake, as in other species, may be linked to many factors, one of which is cannibalism. Although the most abundant prey of this species are crustaceans, throughout all life stages cannibalism is extensive. However, before an examination of the role of cannibalism in the dynamics of this species can be investigated, the diet and consumption rates were calculated. Investigation of population dynamics will these estimates will be used in a sequential population model.

Review of Silver Hake Consumption

Consumption models for stomach content data have been developed over the last fifteen years. Initial work by Bajkov (1935) and Ivlev (1944) and more recently Eggers (1977), Elliott and Persson (1978) and Pennington (1985) has led to a group of models relying on the collection of stomach content weight and laboratory data related to evacuation rates.

The development of a fish consumption model predicated on stomach content data assumes the rate of evacuation is known or can be estimated. The most contentious part of the calculation of consumption rates from stomach content data is the selection of an appropriate evacuation model. Other factors such as temperature effects, and the type, shape and size of the food particle all have an influence on the estimated consumption rates.

There are three basic evacuation models in current use today:

- i) The Surface Area (Fänge and Grove, 1979 and Tyler, 1970):

$$\frac{dW}{dt} = -RW^{0.67} \dots\dots\dots(1)$$

- ii) The Square Root (Tyler, 1970)

$$\frac{dW}{dt} = -RW^{0.5} \dots\dots\dots(2)$$

- iii) and the Exponential (Elliott and Persson (1978) and Pennington (1985))

$$\frac{dW}{dt} = -RW \dots\dots\dots(3)$$

where W = weight (or volume) of food, R is the constant rate of evacuation.

Each model has limitations, but the exponential model has been accepted as most suitable to the greatest number of situations and species (Durbin et al. 1983; Eggers, 1979; Jobling, 1986; Mullen, 1986; Olson and Mullen, 1986; Persson, 1986; Pennington, 1985).

There have been several recent papers reporting consumption rates for silver hake (*Merluccius bilinearis*). Each utilized a different method to calculate the consumption rate. For example, Edwards and Bowman (1979) used caloric values for stomach contents and a surface area model to estimate evacuation rates of the prey. These rates were used to calculate the length of time it took to fully digest certain prey, and the number of meals silver hake could consume in a year was extrapolated. Their model gave a population consumption rate ranging from 1.3 - 5.7% body weight (BW) per day (Table 01).

Pennington (1981 and 1985) used empirical observations of stomach contents to calculate daily consumption rates for silver hake. He estimated that between 1973 and 1976 the average daily consumption for a population of silver hake was $1.30 \pm .47\%$ BW per day.

Durbin and Durbin (1980) and Durbin et al. (1983) used the method of Elliott and Persson (1978) to calculate average daily consumption rates. Like Pennington (1981), they also combined data over several years and calculated consumption rates by season and fish size. Separate gastric evacuation rates were calculated for large prey items (i.e. fish) and small sized prey (i.e. small invertebrates). Meals consisting of large particles were estimated to evacuate at a rate which was 10% that of small particle meals (Durbin et al. 1983). Since they found silver hake less than or equal to 20 cm preyed primarily on invertebrates, while silver hake larger than 20 cm in length feed mainly on fish, separate estimates of evacuation rates for each size group were necessary. For fish in the smaller size group, Durbin et al. (1983) computed a daily consumption rate of 0.8% BW for the spring and 1.27% BW for the fall. Silver hake greater than 20 cm in length were estimated to consume 0.96% BW per day in the spring and 0.53% BW per day in the fall.

Cohen and Grosslein (1982) used the Pennington's (1981 and 1985) model on data from silver hake collected during 1963-1972 from Georges Bank and the Gulf of Maine. They estimated that silver hake

have a daily ration of between 0.6 and 2.2% BW for all prey categories. Daily consumption of fish prey alone ranged from 0.1 to 1.9% BW.

Clay et al. (1984) developed a modification of the Elliott & Persson model using the observed number of prey consumed by silver hake cannibals, the frequency of occurrence of the prey in the diet of the cannibal, the number of days the prey was available, and the number of days to completely digest the prey. They estimated a consumption rate of 4.0% BW per day for Scotian Shelf silver hake, 10-19 cm in length, during the period May to December of 1976-1979.

Vinogradov (1977) estimated daily consumption rates for Georges Bank silver hake from diel experiments conducted during July 1971, 1972 and August, 1972, 1973. Using empirical data his method gave daily ration estimates of 14.2%, 3.5%, 12.2% and 3.6% BW. He also used the same data set and a modification of the Winberg's (1956) mass balance equation to calculate the daily ration. This approach gave estimates of silver hake daily rations of 3.36%, 4.00%, 3.46% and 3.60% BW for the sampling periods, respectively. These later estimates are dependent upon the various assumptions of caloric values for prey species, estimates of oxygen consumption used to calculate Specific Dynamic Action (SDA), and energy expended in the production of reproductive products.

Studies on other species of hake reveal some differences in daily ration and diet compared to silver hake (Table 01). The average daily consumption rate for Pacific hake, *Merluccius productus*, was estimated at 2.5% of body weight (Livingston and Bailey, 1985; Francis, 1983). The diet of *M. productus* adults, unlike silver hake, is mainly Euphausiidae. Cape hake (*Merluccius capensis*) have daily consumption rates much higher than those for silver hake (6.9% at age 1 to 8.8% BW at age 7) (Prenski, 1980). The diet however, is similar to that of silver hake in that invertebrates such as Myctophidae and Euphausiidae constituting the bulk of the diet for fish less than 50 cm in length (e.g. age 5) and hake prey constituting the major portion of food consumed by cape hakes aged 6+.

The role of cannibalism in the silver hake population

The role of cannibalism in the silver hake population has been considered by Clay and Nielson (1985), who use consumption estimates from Clay et al. (1984) to calculate cannibalism mortalities. These cannibalism mortalities were then used as input to a modified Virtual Population Analysis (VPA). The average mortality rate for cannibalism on ages 1-3, weighted by population numbers, was equal to 0.836, which is double the constant natural mortality (0.400) used in most silver hake assessments (Almeida and Anderson, 1981; Waldron and Fanning, 1986a; Fanning et al. 1987).

The ability to reduce the amount of unidentified mortality in VPA results in a more realistic model of the dynamics for the population being considered. Both Clay and Nielsen (1985) and Lleonart et al. (1985) noted significant differences in the results of VPA and fishing mortalities when natural mortality was partitioned into cannibalism and the residual mortalities. When cannibalism mortality at age was included in their models, the overall fishing mortality was reduced, with the estimated terminal F lower than that estimated when cannibalism is not present in the model. The reduction in fishing mortality on younger ages, when cannibalism was included, has implications for management of the fishery. It is the purpose of this paper to use stomach content data to calculate silver hake cannibalism rates and investigate the role of cannibalism in the dynamics of silver hake.

Materials and Methods

A). The consumption model used

The rate of change in fish stomach contents is proportional to the amount of food consumed, and the rate at which it is evacuated from the stomach. That is:

$$\frac{dS(t)}{dt} = F - RS(t) \dots \dots \dots (4)$$

where R is the exponential gastric evacuation rate, S is the stomach contents and F is the rate food is consumed. Integrating and assuming that as the consumption rate approaches 0, the actual amount of food consumed C_t in t hours can be expressed as:

$$C_t = \frac{(S_t - S_0 e^{-Rt})Rt}{1 - e^{-Rt}} \dots \dots \dots (5)$$

where S_t is the stomach contents at time t, S_0 is the initial stomach contents, and t is time (hrs.). This is the classical Elliott and Persson (1978) model of food consumption by fish.

The Elliott and Persson (1978) model assumes a constant rate of food consumption between S_t and S_0 . They extended their model to calculate consumption over a 24 hour period by assuming not only a constant rate of food consumption between each time period sampled, but also that the initial stomach contents were equal to those observed at the end of the 24 hour period. These assumptions may be valid for some fish species, especially those that do not show a diel feeding cycle or where fish do not feed to satiation. Usually this does not apply to wild situations. The assumptions for this model preclude its use for data other than those collected under controlled conditions.

Pennington (1981 and 1985) developed a model which is more suited to field applications than that suggested by Elliott and Persson (1978). Assuming the rate of change of stomach contents can be expressed as in equation 4, then for a time period starting at 0 and of T hours in duration, the average amount of food consumed per hour (C_T) is:

$$\frac{1}{T} \int_0^T F(t) dt \dots \dots \dots (6)$$

where F is the rate of food consumption. Solving equation 4 for F(t) and substituting into equation 6 yields:

$$C_T = \frac{R}{T} \int_0^T S(t) dt + \frac{1}{T} \int_0^T dS(t) \dots \dots \dots (7)$$

which equals after differentiation:

$$C_T = R\bar{S}_T + \frac{(S_T - S_0)}{T} \dots \dots \dots (8)$$

where C_T is the consumption rate for time period T, \bar{S}_T is the average value of the stomach contents S(t) over the period T, R is the gastric evacuation rate, S_0 is the initial stomach contents, S_T is the stomach contents at the end of the time period. In all cases empty stomachs were also included in the calculation of consumption.

If the amount of food in the stomach at the beginning of the period under study is equal to the amount at the end (i.e. $S_T - S_0 = 0$), the Elliott and Persson (1978) assumption, or as T becomes large, equation 8 becomes:

$$C_T = R\bar{S}_T \dots \dots \dots (9)$$

Unlike the Elliott and Persson (1978) model, this model does not assume feeding is constant over a particular time period. By not assuming constant feeding, the model (8) provides a more applied method to

calculate the consumption rate using data collected in the wild rather than from fish kept in a controlled environment. In this context, population estimates of consumption are possible.

An unbiased estimate of S (i.e. $S_{(0,T)}$) can be obtained by choosing random times between t_0 and T, say $t_1, t_2 \dots t_m$, and taking a random sample of fish at each time. The estimated average stomach contents over the time period T is:

$$\hat{S}_{(0,T)} = \frac{1}{m} \sum_{j=1}^m \hat{S}(t_j) \dots \dots (10)$$

where the average stomach contents for the population is the sum of the average stomach contents for all the fish caught at a particular station (k) within the time (m):

$$\hat{S}(t_j) = \frac{1}{k} \sum_{i=1}^k \hat{S}(t_j) \dots \dots (11)$$

Then an unbiased estimate of the average amount of food consumed by the population during this period \bar{C}_T is:

$$\bar{C}_T = R_T \hat{S}_{(0,T)} + \frac{\left(\hat{S}_{(0,T)} - \hat{S}_{(0)} \right)}{T} \dots \dots (12)$$

The variance of C_T (equation 13) for large N was estimated using the method of Snedecor and Cochran (1967; p. 279).

$$\text{var } \bar{C}_T = R_T^2 \text{var } \hat{S}_{(0,T)} + \text{var} \left(\frac{\hat{S}_{(0,T)} - \hat{S}_{(0)}}{T} \right) + \text{var} \frac{\hat{S}_{(0)}}{T^2} \dots \dots (13)$$

where:

$$\text{var } \hat{S} = \sum_{j=1}^m \left(\frac{\left(\hat{S}_{(0,j)} - \hat{S}_{(0,T)} \right)^2}{m(m-1)} \right) \dots \dots (14)$$

Assuming gastric evacuation is represent by equation (4), then the average daily consumption (or ration) is calculated as:

$$C_D = 24R\bar{S} \dots \dots (15)$$

which is the Eggers (1979) modification of the Bajkov (1935) equation.

B). Estimates for model assumptions:

The accuracy of the consumption estimate used depends on the validity of the assumptions underlying the model:

- 1) the rate of gastric evacuation, R, is exponential and proportional to the stomach contents (i.e. a constant proportion of the stomach contents is evacuated per unit time),
- 2) the rate of gastric evacuation is constant for all fish in the target population over the time period being considered.

Durbin et al. (1983) suggested that the rate of gastric evacuation was not affected by either silver hake size or the frequency of feeding (i.e. presence of multiple meals). However, R was affected by ambient temperature and the type of food consumed which probably incorporated some influence caused by differences in the size of the prey (particle size) and the size of the meal. Elliott (1972) observed that temperature will influence the rate of gastric evacuation according to the following relationship:

$$R = ae^{bt} \dots \dots (16)$$

where t is the ambient temperature, a is the intercept which is dependent upon prey type and b is the slope. Durbin et al. (1983) found the slope of equation 16 was very similar for several marine and freshwater

species. Tyler (1970) observed that for the gadoid, Atlantic cod, the exponential gastric evacuation rate of fish prey was approximately 10% that of crustacean prey. Since silver hake is a gadoid with a diet similar to cod, Durbin et al. (1983) assumed evacuation rates to be similar. They calculated an overall intercept 0.0406 for small prey (i.e. invertebrates) and 0.00406 for fish prey with a common slope of 0.111. For the current work, R was corrected using average bottom temperatures for the spring (1979 - 1985), summer (1970-1986) and fall (1979 - 1984) obtained from the Scotian Shelf groundfish surveys (Table 02).

Since digestion continues after capture, a correction suggested by Cochran and Adelman (1982) was employed to adjust stomach content weights as follows:

$$S_c = S_t e^{R(t_s - t_c)} \dots\dots(17)$$

where S_c is the corrected stomach weight, R is the gastric evacuation rate, t_c is the time of capture, t_s is the time stomach was fixed and S_t is stomach content weight at the time of fixation. All stomach content weights were adjusted according to the time between capture and fixation with formalin. During this study all stomachs were fixed within 1 hour of capture by the gear for R/V and up to 3.5 hours after capture by the net for commercial vessels.

Biases in stomach weights due to predator size and the weight of water/ formalin in the stomach, as well as the stomach tissue weight were reduced by the following formula:

$$S_i = \left(\frac{\sum WSi}{\sum (WP_i - WSi)} \times 100\% \right) \dots\dots(18)$$

where $\sum WSi$ is the sum of individual prey weights and WP_i is the body weight of each predator (i).

C). Calculating consumption

The degree to which feeding, and hence estimated consumption rates, varied over seasons (spring-fall), years and age groups was investigated using a hierarchical three way ANOVA (SPSS*) of percent body weight and consumption rates normalized using the arcsine square root transformation (Sokal and Rohlf, 1969). Average percent body weight was calculated from equation 10. The results of this analysis established categories for calculating consumption. Within each category, hourly consumption rate for each age group was calculated for each trawl station, and aggregated by hour. Yearly consumption (\bar{C}_Y) was calculated as:

$$\bar{C}_Y = \bar{C}_D \times \%BW_{prey} \times A_{prey} \times 365Days \dots\dots(19)$$

where consumption/day (\bar{C}_D) was from equation 15 and $\%BW_{prey}$ reflects the observed dietary composition of the predator within a particular category. Availability of prey (A_{prey}) is an estimate of the amount of time as a proportion of the year that the prey is available to the predator. Adult silver hake are not found with juveniles less than 7cm in length. It takes six months for juvenile silver hake to attain this length (Hunt, 1979). In this model 0.5 was assigned for age 0 fish with all other age groups set to 1.0.

D). Investigation of cannibalism in silver hake

a). Cannibalism

Cannibalism in silver hake was identified in 114 cases over the period 1981-1986. There were many situations where stomach contents could have been silver hake, but the advanced state of digestion precluded a definite determination. The influence of year, season and age were investigated using a hierarchical 3-Way ANOVA model.

Estimates of silver hake cannibalism consumption rates at age used stomach content data grouped by season to account for changes in ambient water temperature. These consumption rates were averaged by

day, and the number of prey aged i silver hake cannibal j eats in a year y (\bar{E}_{ij}) was calculated as:

$$\bar{E}_{ij} = \text{Preference} \times \text{Consumption} \times \text{Observed \% BW Prey} \times \text{Availability} \times 365 \text{ DAYS} \dots\dots\dots(20)$$

where

$$\text{Preference} = \frac{\bar{S}_{ij}}{\sum \bar{S}_{ij}} \dots\dots\dots(21)$$

Consumption is the average daily consumption of predator aged j (\bar{C}_j), the Observed % Body Weight Prey is the average percent body weight that prey aged i is of predator aged j for the years 1981-1986 (\bar{S}_{ij}), and the Availability of prey to the predator was determined to be for age 1 prey 50% of the year, while all other prey age groups were set to 1.0.

b). Model

The effects of cannibalism on the silver hake population was evaluated using a modification of Pope's (1972) COHORT analysis. On a cohort basis, the number of prey (P) aged $i+1$ remaining at the beginning of the year $t+1$ is dependent, among other things, upon the average abundance of the predator K aged j during year t , and is expressed as:

$$P_{i+1,t+1} = P_{i,t} - \alpha_{j,i} K_{j,t} \dots\dots\dots(22)$$

where j is assumed greater than i , and $\alpha_{j,i}$ is the average number of prey age i eaten by a single predator aged j during year t .

Cohort analysis requires a matrix of catch at age, estimates of fishing mortalities at age for the oldest age and the last year of catch, an estimate of total mortality and the selectivity at age. These inputs were calculated in Waldron et al. (1988). The number of silver hake cannibalized was considered as removals by another fishery (i.e. a predation fishery) and added to the catch by the commercial fishery.

Since the estimated cannibalism is dependent on the number of fish older than the prey, the calculation was conducted iteratively on a cohort by cohort basis (i.e. along the diagonals of the catch matrix) starting at the bottom left corner of the matrix. Initial estimates of N were made using the catch at age, terminal fishing mortalities, F 's at the oldest age and the partial recruitment from (Waldron et al., 1988).

$$\bar{N}_{i,y} = \{N_{i+1,y+1} + 0.5C_{i,y}\} e^{M_{i,y}} \dots\dots\dots(23)$$

Beginning of the year population numbers N at age j in the last year of the catch at age matrix are estimated using the following algorithm:

$$N_k = (C_k + E_k) \frac{Z_k}{F_k(1 - e^{-Z_k})} \dots\dots\dots(24)$$

where N is the beginning of the year population numbers for each cohort k , and i is the age of the prey eaten.

By definition, total mortality (Z), is the sum of the fishing mortality (F) and mortality from all other causes often referred to as natural mortality (M).

$$Z = F + M \dots\dots\dots(25)$$

If cannibalism is incorporated into the model, M can be partitioned into predation mortality, M_p and a residual mortality M_r and total mortality becomes:

$$Z = F + M_p + M_r \dots\dots\dots(26)$$

For the last year and oldest ages, M_p is equal to zero since the model assumes that small fish do not prey on older fish. However, for the last year M_p is not necessarily equal to zero and must be calculated

using equation 24. For all other ages and years, cannibalism is treated similarly (i.e. a predation fishery). The number of fish removed by predation is related to the number of predators at age and their preference for each prey age group in each year. An estimate of the numbers of silver hake at the beginning of the year y would be:

$$N_{k,y} = (C_{k,y} + E_{i,j,y})e^{M_{Rk}} + N_{k,y+1}e^{M_k} \dots\dots\dots(27)$$

where k is the cohort, y is the year, i is the prey age group, j is the predator age group, $C_{k,y}$ is catch and $E_{i,j,y}$ is the numbers eaten, $N_{k,y+1}$ is the population numbers at age and M_R is the constant residual natural mortality from all other sources except cannibalism. The parameter, M_{Rk} assumes that F is distributed uniformly throughout the year, and more of the fully recruited fish are taken in the first half of the year than the second half. Pope (1972) demonstrated that this assumption performed well for most fisheries when $M < 0.3$ and $F < 1.2$. Pope (1972) found that for F and M larger than these, the final population numbers at age varied by as much as 4.0%. Therefore the anticipated differences in population estimates should be marginal given the potential variance in catch at age and the estimated value of M_R .

Leonart et al. (1985) assumed M_R for Cape hake (*Merluccius capensis*) to be 0.157, or 52% of the total natural mortality of 0.30. Similarly, Clay and Nielson (1985) assumed M_R for silver hake was 0.15 or 38% of the total natural mortality of 0.40. Pope and Knights (1982) assumed that M_R was equal to 0.10 or half of the total natural mortality for cod of 0.20. Adopting the above assumptions, M_R for silver hake was assumed to be equal to 0.20, or half of the natural mortality of 0.40.

The model proceeded iteratively until the following identity was satisfied:

$$\text{Maximum value of } \{Z_{i,y} - Z_{i,y}\}^2 \leq 0.1 \times 10^{-4} \dots\dots\dots(28)$$

where $Z_{i,y}$ and $Z_{i,y}$ are the total mortality in the i th prey cohort in the y th year estimated in the current and previous iteration.

c). Stock recruitment

On several occasions stock-recruitment relationships have been investigated for this stock (Waldron, 1981). All attempts gave less than satisfactory results. The Ricker (1975) stock-recruitment curve was investigated, as Ricker recommends this curve as the most suitable when cannibalism is present. The relationship between the parent stock (spawning stock) and recruitment to the population is;

$$R = \alpha P e^{-\beta P} \dots\dots\dots(29)$$

where R is a measure of recruitment (numbers or biomass), P is the spawning stock size (numbers or biomass), α is a dimensionless parameter, β is the slope with dimensions of $1/P$ and reflects the density dependent factors for the stock-recruitment relationship (Levin and Goodyear, 1980). The maximum level of recruitment for the population is when the spawning stock size (P_m) is;

$$P_m = \frac{1}{\beta} \dots\dots\dots(30)$$

The equation 29 was solved by regressing $\log_e R - \log_e P$ on P such that

$$\log_e P - \log_e R = \log_e \alpha - \beta P \dots\dots\dots(31)$$

where α is the intercept which reflects density independent factors.

d). Yield per recruit

A Thompson and Bell yield per recruit model (equation 32) was used to calculate the Maximum Sustainable Yield (MSY) for the population under two scenarios, cannibalism and no cannibalism. Rivard (1982) provides an APL workspace to compute the Thompson and Bell model as well as SPA and

projections which are used. Partial recruitment of the fish to the fishery for the CANCOHORT model was calculated as the arithmetic average of fishing mortalities at age for 1977 to 1985. The partial recruitment for the COHORT model was from advice given at the 1987 NAFO scientific council meeting (Anon. 1987). Natural mortality was assumed to be 0.4 for the COHORT model, and for the CANCOHORT model this parameter was calculated by averaging M at age for the period 1981-1986. The equation for calculating the yield per recruit is as follows:

$$Y = \sum_{i=b}^m W_i N_i \frac{F_i}{Z_i} (1 - e^{-Z_i}) \dots \dots (32)$$

where Y is the yield, b is the age of the youngest age group, m is the age of the oldest age group, W_i is the weight at age i, N_i is the population numbers at age i and Z_i is the total instantaneous mortality at age i.

e). Impact on $F_{0.1}$ estimates and projections of future population size

In Canada, the recognized management level of fishing mortality is $F_{0.1}$ and was defined by ICNAF as "... the marginal value of the fishing mortality at which the marginal yield per recruit (i.e. the addition to the total yield per recruit resulting from adding an additional unit of mortality) is 10% of the catch per recruit per unit mortality in a very lightly exploited stock. This has been referred to in some documents as F_{opt} . Unless the objective is maximum yield from the stock being considered, irrespective of costs or of the opportunities for increasing catches from alternative stocks, it will be desirable to fish at a level of effort somewhat less than that giving the maximum yield. The choice of the precise point will depend on social and economic factors, but a fairly reasonable guide of where the target level might be in terms of yield per recruit is provided by $F_{0.1}$. This was chosen on the basis that at this level the net production of an additional vessel will be only one-tenth of that of the first vessel to enter the fishery, and that this is probably the limit of economical operations. Ideally these calculations should be made in terms of total yield, rather than yield per recruit. For most stock-recruitment relations the value of $F_{0.1}$ will occur at a lower point relative to the maximum on the total yield curve than on the yield-per-recruit curve." (Anon. 1972).

Computationally, $F_{0.1}$ is estimated iteratively and is the value of F in X which ensures that $X = 0.1 \times SL$, where SL is the slope of the yield to fishing mortality curve.

Projections were run using the APL Fish workspace (Rivard, 1982). The projection routines use the Baranov catch equation (Ricker, 1975) which estimates the population size at age given inputs of fishing mortality, total mortality and population size as;

$$C_i = F_i (1 - e^{-Z_i}) \frac{N_i}{Z_i} \dots \dots (33)$$

where C_i is the catch at age i in the next year, F is the fishing mortality for the year, N is the beginning of the year population size and Z is the total natural mortality.

The projection requires a level of fishing mortality which is usually set at $F_{0.1}$, the average weight and partial recruitment at age for a period of years, the population size and catch at age for the most recent year and a level of recruitment. Recruitment for the projections presented here was calculated as the geometric average of the years 1977-1985. The years 1977-1985 were selected because the catch at age data was collected and aged by Canada, as opposed to samples supplied by other countries, and as such was considered the most reliable estimate of the age structure in the catch.

Results

A). Consumption by silver hake

Collection of gut contents over the period, 1981 to 1986 resulted in observations made of over 11,000 fish (Table 03). Average %BW for selected prey groups indicate that as silver hake grow old, the

diet switches from small invertebrate prey (i.e. *M. norvegica*) to larger fish prey (Table 04). This switch in diet happens between ages 5 and 6. Cannibalism was noted in fish as young as 1 year of age, and begins to dominate the diet between the ages of 4 and 5, increasing with age (Figure 01).

An ANOVA comparing year, season and age group effects on the percent body weight and consumption estimates were run. Interactions were significant for all prey categories except year by age and season by age for fish prey. The results show significant yearly and seasonal effects on percent body weight for all prey types eaten. Age effects are not significant ($p=0.052$) at the 5% level (Table 05). However, there are some interactions between age and year which makes the results for age suspect. Significant differences in all interaction terms for invertebrate prey which will influence further interpretation of the ANOVA results for this prey group. Fish prey have no significant year by age or season by age interactions. Age effects for fish consumption are not significant at the 1% level.

Consumption estimates (%BW/day) were stratified by year, season and age group, based on the significant results of the ANOVA above. These computed consumption rates were again tested by a hierarchical 3-way ANOVA for year, season and age group effects (Table 06). Invertebrate consumption was significantly different for year, age and season. Of particular interest to this study was that fish consumption is significant for age only, and is not variable over years nor season for the data set investigated. Interaction terms for fish consumption were also non-significant.

Estimates of mean total daily consumption by silver hake remained consistent for each age except ages 9 and 10, where consumption was half of that observed for other age groups (Table 07). Variance around the mean consumption was high for all ages and seasons.

Seasonal consumption rates are compared in Figure 02. Consumption during the winter months, compared to that calculated for other seasons, showed that consumption by ages 1 and 4 was the highest while consumption by ages 5 and 7 was the lowest. Indeed, consumption rates estimated for age 1 during the winter are the highest observed for all age groups. However, sample sizes for the winter period were small and more observations are required before definitive statements can be made on consumption rate differences. What is important is that silver hake continue to consume prey during the winter contrary to suggestions by Clay et al. (1984).

Consumption rates for fish aged 1-3 is highest in the fall, while fish aged 4-6 and 10 show the highest consumption rates are during the spring just prior to spawning. Fish aged 7-9 have the highest consumption rates during the summer. Consumption for older fish (age 5+) decreased in the fall, while fish ages 1 to 4 increased their food consumption during this season.

Daily consumption for the fastest growing portion of the population, age 1, is the highest in the winter, remains constant at a lower level during the spring and summer, then increases in the fall. In general, consumption decreases after age 6 and continues to decline with age (Table 07). In the spring, silver hake aged 8 years and older have the lowest consumption rates.

B). Cannibalism in the Scotian Shelf silver hake population

Cannibalism by silver hake is directed on age groups 0-4 (Table 08). The relationship of size of prey to size of predator was noted by Waldron (1988). On average, silver hake cannibalized prey which were half its own body length. The difference in length between an age 1 and 2 silver hake is much greater than that between older ages. After age 5, the age - length relationship for silver hake is nearly asymptotic (Hunt, 1979).

Preference at age (Table 10b) shows that ages 2-4 prey heavily on recruiting fish while ages 5-7 focus predation on 2 year old silver hake. Ages 8 and 9 silver hake concentrate the major portion of their consumption on age 3 and 4 individuals. The shift to a highly cannibalistic diet (3-5 times body

weight/year) for ages 6 to 8 is shown in Table 10e. Diet analysis from Table 06 reveals the increasing contribution cannibalism makes to the diet. By stomach content weight, cannibalism constitutes 31% for age 6, 41% for age 7, 44% for age 8 and 63% for age 9 and older. Predation on large Mollusca, in particular squid, is 20%, with crustaceans making up the remainder of the diet.

The high cannibalism rate on age 1 fish occurs in the winter, when the young of the year descend from the upper water layers to mix with the rest of the population. This is also a time when other prey are less abundant, and to supplement their diet, age 1 fish become cannibalistic (Table 07 and Table 8). Again size selection is evident for this age group during the winter, when recruiting year classes are approximately half the body length of age 1 silver hake. However, size selection does not seem to apply for the older cannibals. Cannibalism on age 0 increases with age (Table 10h) while it is relatively unimportant to the diet of fish in age groups 2 and 3.

C). Results from CANCOHORT model

Output from the CANCOHORT model is presented in Table 09, and for the COHORT model in Fanning et. al., 1987. The calculated numbers at age for silver hake were higher at ages 1 and 2 in CANCOHORT because of increased total mortality (Figure 03). However, by age 3 the CANCOHORT model estimates less silver hake at age. It seems that by incorporating cannibalism mortality in the SPA higher recruitment estimates result, with survival to older ages being less than that estimated by the COHORT analysis. A serious overestimate of the number of age 4+ fish would result without cannibalism mortality being considered. Population biomass estimates from the two models exhibit similar patterns.

Natural mortality from the CANCOHORT model is composed of a constant residual and an estimated cannibalistic natural mortality rates. Cannibalism mortality is much higher than the usual value for natural mortality of 0.4 for ages 1 and 2, and is below 0.4 for age 3 and 4 fish (Figure 04). Fish age 5 and older were assigned a constant natural mortality of 0.400. Using these input natural mortality levels, the population weighted natural mortality for the CANCOHORT model is calculated as 0.431, which is slightly larger than the population natural mortality of 0.400 used in recent NAFO assessments and is the value recommended by Terre and Mari (1977). Therefore, the assignment of a natural mortality value of 0.400 for ages 5 and older is justifiable in the context of accepted assessment practices by NAFO.

The large cannibalism mortality for age 1 fish in 1985 and age 2 fish in 1986 (i.e. the 1984 year class) may be the model's reaction to the large 1983 year class. Since there are more fish, cannibalism mortality will appear high. Fishing mortality on age 2 fish in 1986 is lower than the average for age 2 fish in other years which may worsen the estimation of the 1984 year class at age 1 in 1985. In estimating the population size for this stock, the size of the most recent year classes is always difficult. It will not be until a few years from now that an improved size estimate for the 1984 and 1985 year classes will be possible.

From 1970-1976, fishing mortalities (F) at ages 1 and 2 were often less for the CANCOHORT model (Figure 05). Fishing mortalities at age 3 were usually higher for the model including cannibalism because of the lower population numbers at age 3 estimated by the CANCOHORT model. Fishing mortalities on age 4 were marginally higher when cannibalism was included. A different pattern emerges for the period 1977 to 1983. Fishing mortalities for ages 1-4 from the CANCOHORT were similar to, or less than, those calculated from the COHORT analysis except age 1 in 1980. The change in fishing regime from 1977 to the present lowered the F's at age from those observed prior to 1977, when the large fleets were using smaller codends and expended more effort in the fishery. Also, since the model was not calibrated, the selected terminal fishing mortality of 0.350 may be too high for the current fishery.

The large differences in fishing mortalities for age 1, 3 and 5 silver hake in favor of COHORT suggest that fishing mortalities calculated from COHORT may be compensating for some other form of

mortality such as cannibalism. This large difference in F is especially evident from 1984 to 1986. Cannibalism mortality for ages 1 and 2 show a similar erratic behaviour from 1984 to 1986, with large changes in mortality (Figure 04). One possibility for this behaviour in mortalities could be the way in which the CANCOHORT manages large year classes. A comparable pattern of cannibalism mortality can be seen for 1973, when the large 1971 and 1972 year classes were in the 1973 fishery. As these year classes move through they fishery they become formidable, exerting increased cannibalistic pressure on subsequent juvenile fish. Then, the high abundance of the 1983 year class at age 2 in 1985 may explain the unusually high cannibalism mortality on age 1 silver hake in 1985 (Figure 04). This pattern of fishing and cannibalism mortalities from 1984 to 1986 may be dampened as new catch data are added to the catch at age matrix.

a). **Impact on recruitment**

The number of age 1 fish estimated by the CANCOHORT model is often more than that estimated by the COHORT model (Figure 06 and Table 09). This is as expected, since more fish must be present to account for the large increase in natural mortality on age 1. The size of the 1984 year class estimated by CANCOHORT is slightly lower than the abundant 1983 year class, the third largest in the series. This changes the 1984 year class from one of the smallest, as estimated from COHORT, to the fourth largest. However, the size of the 1984 year class in 1986 from CANCOHORT is below that estimated by COHORT. It seems that the cannibalism mortality exerted by the very large 1983 year class at age 2 and 3 in 1985 and 1986 respectively has controlled the success of the 1984 year class. The 1985 year class is expected to exert similar pressures on subsequent recruiting year classes as it ages.

A more convincing stock-recruitment (S-R) relationship is shown for population estimates from CANCOHORT (Figure 07) compared to those from COHORT (Figure 08). The data series does not include the 1984 and 1985 year classes because of the uncertainties in the estimation of their actual size at age 1. The 1969-1971 year classes were also excluded because the catch at age was calculated from an average age length key and presumably does not represent the actual population structure. The 1972 and 1973 year classes were excluded because the catches in the 1973 fishery may not have been all silver hake (Waldron et al. 1988) making the number of recruits surviving from the 1972 spawning artificially higher.

The improvement in the S-R relationship is noted for the CANCOHORT model. The large 1983 year class is very prominent. Juvenile surveys indicate that the 1981 year class is the largest seen in the survey. That is not true for this analysis, although it is one of the highest. The S-R from CANCOHORT shows similar recruitment estimates for a wide range of spawning stock size. The S-R for COHORT suggests some asymptotic relationship where the Beverton and Holt model would be most appropriate (Figure 08).

Peak recruitment from regular COHORT is not apparent from Figure 08 but may be near a spawning stock size of 114,000 (t). The S-R from CANCOHORT estimates the spawning stock size required for peak recruitment is closer to 94,000 (t). For less spawning stock biomass, CANCOHORT estimates larger recruitment. Also, year classes which were thought to be poorly recruited to the population are estimated to be larger using the CANCOHORT model and are similar in size. Qualitatively, there seems to be an overall improvement in the stock-recruitment relationship by including cannibalism in the SPA model (Figures 07 and 08).

b). Production

The amount of new growth present in the population over the year is referred to as production. Total production¹ estimates from CANCOHORT are higher than those from COHORT (Figure 09). Prior to 1977 surplus production (i.e. the amount of production in excess of a population equilibrium which can be harvested) is slightly higher for the CANCOHORT model (Figure 10). After 1976, surplus production for the stock is generally lower for the CANCOHORT model. A similar pattern was seen for the net production for the stock which was lower in the CANCOHORT than the COHORT model (Figure 11). However, as with the surplus production estimates, they track each other very closely. Cross over of the two curves are due to the estimated size of recruiting year classes. For example, 1973 year class at age 1 in 1974 is estimated to be much larger by the CANCOHORT model (Table 3.14 and Table 09). Net production dropped in 1973 primarily due to the sharp increase in the 1973 catch, which was almost three times the average for the pre 1977 fishery.

The ratio of production to biomass (P/B) provides a measure of the turnover of production for the population. High P/B ratios indicate, among other things, a stock which has high recruiting biomass and a concentration of growth in the earlier age groups. Silver hake P/B ratios were highest in the early 1970's when the fishery was most active (Figure 12). The reliability of the Soviet catch statistics in the early 1970's has been previously discussed. This has probably caused some of the production estimates to exceed 1.0 for that time period. Disproportionate catch at age for 1973 would result in an overestimate of the population size in 1972, and hence the larger Production and P/B ratios as seen in Figures 09 and 12. The P/B has been oscillating between 0.75 and 0.97 since 1977, due to several good year classes. This high level is not seen in many other species, such as cod, where recruitment to the fishery is at age 3 (Rivard, 1984).

The inverse of the P/B is the time it takes for the population to replace its biomass. Silver hake has a fast turnover rate (.9 - 1.9 years) compared to other gadoids in the northwest Atlantic (Figure 13). Haddock and cod stocks have a turnover time of 2 years while redfish are between 6 and 8 years (Rivard, 1984). Herring has highly variable turnover times greater than 10 years and in the case of the Eastern Newfoundland herring, the turnover time can be as high as 25 years. For silver hake, the inclusion of cannibalism reduces the turnover time by almost half a year. In years with sizable year classes, such as the large 1981 and 1983 year classes at age 1 in 1982 and 1984 respectively, the turnover rate approaches 1 year.

c). Yield per recruit and projections of future catch

Several inputs to the projection procedure are already different between the two SPA models (Table 11a). The numbers at age for 1986 are obviously different, mean weights at age and the catch for 1986 will be the same, but perhaps the most important differences are the partial recruitment, the level of expected recruitment, variable natural mortality and the $F_{0.1}$ fishing mortality.

The yield per recruit model of Thompson and Bell gave lower yields for the CANCOHORT model compared with those of the regular COHORT model (Table 10a,b and Figure 14). The partial recruitment pattern is different when cannibalism, and its associated changes to the inputs to the yield per recruit model, is included in the model which affects the calculated $F_{0.1}$ and F_{MSY} (fishing mortality at Maximum Sustainable Yield). The resulting $F_{0.1}$ of 0.4366 is below the $F_{0.1}$ of 0.530 from COHORT and will have implications on the TAC advice.

¹ See Rivard, 1982 for details on equations used to calculate total, surplus and net production.

Projection of future catch using the population structure from CANCOHORT and COHORT provides fisheries management scientists with an understanding of how cannibalism effects future yields and the structure of the population. The results of several projections are found in Table 11b. Three scenarios were considered. The first two used standard inputs derived from CANCOHORT and COHORT. The third scenario assumed inputs from a standard COHORT, except that variable M was used instead of a constant M of 0.400. This was used to investigate the potential amount of over fishing which would result when cannibalism was not considered during the assessment of the 1986 population size by NAFO.

Comparison of scenarios 1 and 2 show that average recruitment from 1977- 1985 (age 1 fish) is almost double for the CANCOHORT (1.7 billion) compared to the COHORT (1.0 billion) model. Natural mortality was averaged at age for 1977-1985 for the CANCOHORT model (Table 10b), and shows such mortalities are higher than 0.400 for ages 1 and 2. The $F_{0.1}$ for the CANCOHORT model is 20% less than that calculated for the COHORT model and reflects the mortality differences between the two models. By 1988 the initial doubled recruitment from CANCOHORT is quickly dissipated as the large 1983 and 1985 year classes go through the fishery. Population numbers and biomass for the two projections are very close, which means the computed catch for 1989 is 7% lower when cannibalism is included in the model. Without above average recruitment, by 1989 both models predict surplus production well below that observed in the 1986 fishery and by 1990 both are predicting the same catch. Assuming a higher $F_{0.1}$ (0.53) and a variable M due to cannibalism, scenario 3 shows that the 1989 projected catch could increase from 174,000 tons to 189,000 tons with only a slight reduction in overall population size. Loss of biomass from cannibalism is reduced by harvesting more of the cannibals, which is reflected by an increase in surplus production. The projected increases in yield from the CANCOHORT model were not realized in the COHORT model because cannibalism was not included as one of the projection parameters.

Discussion

A). Consumption rate estimates

Of direct benefit to fisheries management is the refinement of natural mortality rates and the provision of more precise estimates of the size of recruiting year classes as well as projected catch. A method to improve these estimates is to utilize stomach content data and foraging behaviour of the species being considered. However, some biases are inherent in consumption estimates when either bioenergetic or field oriented models are used. For example, specimens which have regurgitated must be eliminated from the data set, hence reducing the number of observations and precision of the diet estimate. The ambient temperature is perhaps one of the single most important considerations and where possible was collected and used to modify estimates of evacuation rates. Seasonal temperatures associated with silver hake varied little over the time period investigated. What was surprising was the similarity in the standard errors of the estimates. This low variability in temperatures in areas frequented by silver hake, i.e. along the shelf, have been observed in recent works by Petrie and Loder (pers. comm.). However, over the remainder of the Scotian Shelf there are observed seasonal differences in bottom temperatures (Sinclair et al. 1987 and Drinkwater and Trites, 1987). The calculated average bottom temperatures show that silver hake have a preferred temperature range between 5°C and 9°C which is lower than those (7°C - 11°C) suggested by Scott (1982). Although perhaps not necessary, digestion rates were adjusted by this temperature difference to be internally consistent with the prevailing theories (Elliott and Persson, 1978).

Differences in digestion rates, associated with various food types were incorporated into the model as either small (usually invertebrates = 0.1) or large (fish = 0.01) prey. These estimates of consumption rates, from Durbin et al. (1983), were lower than those used by Prenske (1980) (adapted from Jones, 1974)

for Cape hake *Merluccius capensis* where digestion rates were 0.09 and 0.20 for fish and small crustaceans. Prenski calculated evacuation times of 3.1 days for fish prey and 1.3 days for crustacean prey.

Clay et al. (1984) suggested the evacuation time of 1.5 days for small fish prey and 3.5 days for large fish prey based on laboratory observations reported by Tyler (1970) and MacDonald et al. (1983). Using Elliott and Persson's (1978) observations on the time to 99% evacuation of a meal I calculated the number of days for a large and small prey meal. For large prey;

$$Time_{0.99} = e^{-\left(\frac{0.09}{0.18}\right)} = 2.73 \text{ days} \dots\dots(34)$$

and similarly for small prey;

$$Time_{0.99} = e^{-\left(\frac{0.20}{0.18}\right)} = 1.11 \text{ days} \dots\dots(35)$$

Edwards and Bowman (1979) proposed that evacuation time was equal to the prey length squared over the square root of the meal size. Using their approach, I calculated that the evacuation time for a 30 cm prey ingested by a 54 cm silver hake, would be 2.93 days.

These estimates fall within the values presented by other authors and support the use of the above digestion rates.

Consumption estimates for silver hake here are within the range presented by other authors (Table 01). Georges Bank silver hake were estimated to have consumption rates ranging from 0.8 - 1.27 percent body weight per day. Scotian shelf silver hake are estimated here to have a consumption rate of between 1.28 and 3.30 percent body weight per day (Table 10d). The composition of the diet is however quite different between the two areas which may account for the differences in consumption rates per day. On the Scotian Shelf silver hake prey heavily on invertebrates while on Georges Bank the major prey is fish. The digestion time of fish prey is ordinarily longer than the time required to evacuate invertebrate prey. This is noted when consumption rates are compared by age groups. Age 9 silver hake have a diet composed mainly of fish (85% by body weight) while age 3 silver hake have a diet composed primarily of invertebrates (Euphausiids). The computed daily consumption for age 9 silver hake is 1.28 percent body weight per day compared to 2.67 percent body weight per day for age 3 silver hake. Some of this observed difference may be related to differences in growth rates and metabolism as silver hake becomes older.

The selection of the appropriate model is dependent on the data set and the methods used in data collection. A review of the available methods recommends that the methods of Elliott and Persson (1978) and Pennington (1985) appear to be similar and appropriate for the majority of stomach collected in the wild (Eggers, 1979, Jobling, 1986, and Mullen, 1986). The Elliott and Persson (1978) and Pennington (1985) models have no meal size requirement (i.e. size of meal does not influence the estimated consumption rate). These models do, however, require reliable information on the gastric evacuation rate. The use of a model other than the exponential requires some consideration of the meal size and its effects on the rate of digestion, which may not be proportional to meal size (see Mullen, 1986, for a review of other models).

Multiple meals were considered to bias estimates of consumption (Clay et al. 1984). Mullen (1986) found that sampling of consecutive meals does not influence the calculation of the gastric evacuation rate. Persson (1986) showed that even though retardation in digestive rates for subsequent meals occurred in the perch, *Perca fluviatilis*, the Elliott and Persson (1978) model gave the best fit to the data. The attractiveness of the exponential model is that each observation of stomach content weight is representative of that instant in time and as such, the occurrence of multiple meals has little effect on the estimate of evacuation.

Elliott and Persson (1978) concluded that the accuracy of their consumption model decreased if the sampling interval increased beyond 3 hours resulting in erroneous estimates of the daily food consumption. Such estimates are quite often below the actual value. Elliott and Persson indicate that in certain cases the results obtained using equation (7) may underestimate actual consumption by more than 10%. Eggers (1977) also observed that collecting samples spaced at large intervals could bias the results with as much as a 40% increase in the estimate of consumption. All samples used for this analysis were aggregated to 3 hour period to reduce estimation errors for the model. Pennington found this procedure was appropriate and resulted in minimal loss of accuracy.

Negative consumption rates can occur when using the exponential model fitted with data collected from the field. One reason for negative consumption rates is underestimation of the exponential rate of gastric evacuation. However, negative consumption rates were not observed here, and as such supports the application of the model used here plus the gastric evacuation rates from Durbin et al. (1983).

The various MANOVAs indicate that feeding on fish prey varies little between years and seasons, and hence fish consumption estimates over the sampling period 1981-1986 can be grouped into a single average yearly consumption estimate for each age group. This result is not surprising given earlier work done on the stability of species assemblages on the Scotian Shelf. Mahon et al. (1984) studied the Scotian Shelf fish community structure using March, July and October stratified random groundfish research vessel surveys. They observed high similarities between years for fish communities on the Shelf and Slope areas. Indeed they state the "... striking observation on the analysis of the summer surveys is the similarity of species and site groupings from year to year" and the "... overall picture is one of a system in which the species distributions are strongly aligned with the physical environment, and consistent through time". Thus, the application of an average daily consumption rate to years outside the sampling period seems reasonable in light of Mahon et al.'s (1984) statements.

B). Cannibalism in the silver hake population

Silver hake are well known to be cannibalistic (Langton and Bowman, 1980). Cannibalism in fish populations is one method the population has of reducing the impact of food deprivation. In other words, the population always carries its energy reserves in the form of smaller members of the group. This strategy has been adopted by several other marine species (e.g. the squid, *Illex illecebrosus*, Hirtle, 1981). This is one component of Optimal Foraging Theory where there is a maximization of energy return to the predator population for each prey encountered (Charnov and Orians, 1973).

The study of cannibalism as a life history strategy requires an understanding of the underlying mechanisms which create cannibalism. Earlier this century cannibalism studies were conducted on the flour beetle *Tribolium*. Field work on cannibalism has been rather limited and often unrewarding. Some authors suggest that cannibalism observed in the laboratory is simply a reaction to stress caused by the experimental environment, and such studies do not support field observations (see Fox, 1975 for a review) although this view is not shared by all researchers (Charnov and Orians, 1973 and Leonart et al. 1985). Regardless there are several situations where cannibalism may occur;

1. When food becomes a limiting factor,
2. When the density of the population confounds the availability of other foods. There is often a proportionate relationship between the incidence of cannibalism and density of the prey (Holling, 1965 and 1966),
3. Behaviour of victims. As abundance increases, fish often form aggregations which stimulate cannibalism or attacks by cannibalistic adults,
4. Hunger or stress of the animal. This is difficult to prove and is rarely reported reaction,

5. Availability of victims. Weakened prey as a result of disease or other attacks are vulnerable to cannibalism and indeed may provoke it, and
6. The size of the predator and its prey may also have an impact on the degree of cannibalism observed.

Some of these factors may occur in the silver hake population, but are difficult to detect using the data set provided here. Most cannibalistic species are generalists, preying on a wide variety of other species. When the annual diet is considered, cannibalism in most age groups contribute only a small fraction of the overall food consumed. However, when isolated to particular age groups, the influence of cannibalism on the silver hake population was observed to be very significant. There is an observed pattern of increased cannibalism to increasing recruitment abundance based on the results from the CANCOHORT model. Large year classes, such as the 1973 and 1983, experience moderate cannibalistic mortality, yet as they age they suppress recruiting year classes. The 1984 year class has been reported as very weak (Waldron et al. 1988). As shown in Figure 04, the large 1981 and 1983 year classes are of sufficient age in 1985 to exert considerable cannibalism mortality on the 1984 year class, hence regulating its size. In the silver hake population a dominant year class can suppress recruitment for a number of years until that year class disappears. Similar observations have been reported for bass, walleye, perch and sardine (Polin, 1981).

Differences in the consumption and diet at age for silver hake was investigated by MANOVA. Age differences were noted and consumption rates were computed by age. These age estimates show that silver hake switches from invertebrate to fish prey between 4 and 6 years of age. The preference between fish and invertebrates may be related to visual clues as seen in other fish species such as salmon. Eggers (1982) suggested that the term, dietary preference, was a more or less tautological phrase for that component of prey selection which cannot be attributed to differential rates of prey encounter and evasion.

Examination of the length of silver hake cannibals to silver hake as prey showed that silver hake were cannibalizing fish which were roughly one half their own body length. The highest feeding activity was noted to occur during the dusk and dawn period, suggesting that silver hake are reacting to clearer visual targets as the silver hake school breaks up and fish leave the bottom. This targeting on a particular size range is associated with part of the Optimal foraging theory of apparent size. Eggers (1982) proposed two models to describe a similar observation made on salmon. These were the Apparent Size and Reactive Field Volume models. Simply stated, these models suggest that predators react to prey size within its visual field that are of a particular size. This is the apparent behaviour silver hake exhibit. As the body size increases, smaller prey such as most crustaceans fall below a critical threshold size and their importance in the diet falls off. As the fish becomes larger, other fish become the only prey which are within the visual parameters. Silver hake prey on *Illex illecebrosus*, a species whose size is similar to silver hake, when it is abundant and readily available suggesting that silver hake are concentrating foraging activity on a size basis.

a). Impact on Assessment of Resource Size

i). Comparison with other Scotian Shelf models

The CANCOHORT model presented here provides population estimates which are often much less (most often by an order of magnitude) than those presented by Clay and Nielsen (1985). The major difference between the two methods of estimating the number of prey eaten is the assumptions on consumption rates. Clay et al. (1984) did not calculate a consumption rate based on stomach content weights, but rather used estimates of evacuation times from the literature combined with empirical observations on the average number of silver hake in the gut. This was used in the following equation to

estimate the number of silver hake each cannibal could eat in one year.

$$\text{Number Eaten} = \frac{\text{Mean Number Of Hake In Gut} \times \% \text{ Frequency Of Occurrence} \times \text{Season} \times 365 \times \text{Geographic Overlap Of Predator And Prey}}{\text{Evacuation Time}} \dots (36)$$

Clay et al. (1984) assume an arbitrary set of three evacuation estimates, one each for age 1, 2 and 3 silver hake prey. This assumption ignores observations of the daily consumption rate per fish which is a function of stomach content weights adjusted for body weight. As shown in equations 34 and 35, the time to complete evacuation is a function of the instantaneous evacuation rate R. Since the estimates for silver hake from equation 34 are similar to Clay et al.'s estimates for age 2 prey, then R must be similar to that used here. Therefore, assuming an age 2 silver hake has a mean length of 25 cm and a mean weight of 100 grams and the expected predator, based on observations presented earlier on size related predation, is expected to be approximately double the size of the prey. This would imply an age 9 silver hake of an average length equal to 54 cm and a body weight of 500 g (Waldron et al. 1988). Continuing the argument, the average weight of silver hake evacuated per day would be $100\text{g}/2.5 \text{ days} = 40\text{g/day}$ evacuated. This represents $(40\text{g}/500\text{g}) \times 100\% = 8\%$ body weight per day which is roughly 6 times that estimated here (Table 10d). It is obvious that Clay's method will overestimate the number of prey eaten. It would seem that the method used by Clay et al. (1984) compared to estimating consumption based on stratification of the day and computing the average percent body weight in each strata seems an unwarranted and dangerous simplification of the consumption model. The unassuming use of average numbers of fish, as in equation 36, ignores any sophistication in consumption models developed from the research of Elliott and Persson (1978), Jobling (1981 and 1986), and Eggers (1977 and 1979) to name only the more notable.

ii). Impact on mortalities.

Fishing and natural mortalities were modified by the inclusion of cannibalism in the SPA. They are of course sensitive to the estimated consumption rates and preferences adopted. Monitoring of these parameters should be continued each year, although the number of samples required will be less than those presented here.

Fixing natural mortality at 0.400 for COHORT analysis results in large and variable fishing mortalities because it alone accounts for all other mortalities in excess of the natural mortality of 0.400. The assumption of a constant residual natural mortality in the CANCOHORT model has resulted in decreased natural mortality for age 3 and 4 silver hake. Despite this decrease, total mortality is slightly less than that computed from COHORT analysis. For age 3 silver hake, the decreased natural mortality is influenced by the assumption they are not fully recruited to the fishery in CANCOHORT.

The result of such high mortalities on ages 1 and 2, would be higher than expected estimates of recruitment. Pope and Knights (1982) noted that such high recruitment estimates could obscure a stock-recruitment relationship. The opposite was shown for Scotian Shelf silver hake where the stock-recruitment derived from CANCOHORT gave a more plausible relationship than that obtained from COHORT. This is in contrast to several attempts by Waldron (1979), Anderson (1977) and Hennemuth et al. (1980) to estimate a stock-recruitment relationship for silver hake. Waldron (1981) showed that the Beverton and Holt model provided the best fit to the data. Anderson fitted a Ricker parabola to the stock-recruitment curve, although the relationship showed imagination on the part of the author. Both of these stock-recruitment relationships relied upon estimates of the recruiting year classes, which in the case of most SPA models are highly variable.

The improved stock-recruitment relationship from CANCOHORT is symptomatic of the deficiencies in SPA where natural mortality is fixed. The inclusion of cannibalism has improved the stock-recruitment relationship by describing some of the large differences between recruitment and spawning stock biomass

seen when COHORT was used. The pattern of stock-recruitment is more of a parabola than an asymptotic relationship, and the Ricker stock-recruitment curve seems most appropriate.

Cannibalism by large year classes provides some of the explanation why subsequent year classes are poorly recruited. One example of this was the small 1984 year class, which followed the large 1981 and extremely large 1983 year class. Continued exploration of the stock-recruitment relationship may provide another tool to determine the long-term influence of cannibalism on population fluctuations. A similar approach was instituted by MacCall (1980) for the northern anchovy, *Engraulis mordax*. MacCall found that the standard Ricker curve required modification in order to accommodate cannibalism. Pope and Knights (1982) made a similar observation for several North Sea species.

The silver hake population was assessed at 0.8 million tons for the 1987 biomass, with a spawning stock biomass (age 3+) of 209,000 tons (Anon., 1988). Since maximum recruitment from the stock-recruitment curve is near 114,000 tons, the Scotian Shelf silver hake population could sustain a reduction in half of its biomass before recruitment would begin to decline. However, caution is warranted because similar recruitment levels are possible from quite different spawning stock sizes (e.g. 1982 and 1984).

iii). Impact on population production

The low turnover rates seen in silver hake are indicative of a stock which depends on recruiting year classes. The regular oscillations in the turnover rate since 1977 is clearly matched to large year classes - the larger the recruiting year class the lower the turnover time. Unfortunately, the amount of data presented here does not permit a rigorous time series analysis. However, the pattern is so regular it is tempting to speculate on future recruitment success. There is a clear 2 to 3 year cycle in recruitment with the large 1978, 1981, 1983 and 1985 year classes all resulting in low turnover times. Given this cycle, the 1987 or 1988 year class may be higher than average. Waldron et al. (1988) reported results for the 1986 and 1987 year class sizes. The 1986 year class was similar in size to the large 1983 year class in the juvenile surveys. At age 1 in the summer research vessel surveys, the 1986 year class was 80% that of the 1983 year class and 50% greater than the low 1984 year class. This implies that the turnover time for the 1987 estimate should be higher than that observed for the 1986 estimate. This is what Waldron et al. (1988) found for the turnover rate in 1987. Prediction of incoming year classes may be enhanced using this method once a longer time series exists.

b). Impact on Projections and management strategies

The partial recruitment, a function of the fishing mortality, did change. The inclusion of variable natural mortality at age lowered the $F_{0.1}$ by 20% and the drop in average yield per fish was as expected. The fishery can never obtain the same yield per recruit regardless of the amount of effort. Projected stock sizes are very similar from both models, but losses in potential yields result if the input parameters are from the COHORT model. Using the $F_{0.1}$ estimated in Waldron et al. (1988) to fish the silver hake population estimated by CANCOHORT has no appreciable affect on future yields of silver hake and indeed suggests that silver hake can sustain a large fishing mortality for a short period of time.

Utilization of the silver hake resource by the fishery is important because of the high cannibalism rates of older fish. Harvesting of older fish would reduce the recruitment dampening effects of cannibalism.

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Table 01. Consumption rate estimates from the literature.

Authors	Consumption rate (% Body Wt. per day)
Silver hake Studies	
Clay et al. 1984 Small fish	4.0
Durbin et al. 1983	0.8 - 1.27
Edwards & Bowman, 1979 Small fish Large fish	1.3 - 5.7 0.53 - 0.96
Cohen & Grosslein, 1982 Fish prey All prey types	0.9 - 1.9 0.6 - 2.2
Pennington, 1981	1.3
Vinogradov, 1977 Stomach contents Winberg method	3.5 - 14.2 3.36 - 4.0
Other hake Studies	
Livingston & Bailey, 1985 (Pacific hake)	2.5
Prenski, 1980 (Cape hake) Age 1 hake Age 7 hake	6.9 8.8

Table 02: Average bottom temperatures for the Scotian Shelf, evacuation rate and correction of stomach weight for sampling time.

Season	Average Temperature (°C) (± std.)	R Small Prey (a=0.0406)	R Fish Prey (a=0.00406)	Correction for Sampling time (small prey) and source		Correction for Sampling time (fish prey and source)	
				R/V	Com.	R/V	Com.
Winter	7.2 ± 2.3	0.090	0.009	1.094	1.197	1.009	1.023
Spring	7.8 ± 2.3	0.097	0.010	1.102	1.274	1.010	1.025
Summer	7.6 ± 2.1	0.094	0.009	1.099	1.265	1.009	1.023
Fall	8.3 ± 2.3	0.102	0.010	1.107	1.290	1.010	1.025

* source

R/V = research vessel
Com. = Commercial vessel

Table 03: Stomach collections of silver hake (numbers) on the Scotian Shelf.

Season	YEAR													
	1981		1982		1983		1984		1985		1986		Total	
	Food	Empty	Food	Empty										
Winter			12		6		1	8		12	121	15	140	
Spring	284		655	25	1534	676	702	622	284	613	315	743	3774	
Summer	966	269	152	16	688	177	187	104	34	312	437	249	2464	
Fall	117		79		440	46	907	49		13		75	1543	
Total	1367	269	898	41	2668	899	1797	783	318	950	873	1082	7921	4024

Table 04: Average percent body weight of major prey categories in the gut of silver hake by age groups.

Percent Body Wt.	Age Group								
	1	2	3	4	5	6	7	8	9
Silver hake	1.8	0.6	0.7	3.9	17.9	24.9	52.7	51.5	54.5
M. norvegica	32.0	46.4	30.0	24.9	7.3	2.4	1.2	0.0	0.0
Fish	4.4	15.9	30.3	32.3	39.1	62.6	71.0	81.6	85.3
Invertebrates	83.1	73.9	59.6	58.1	56.8	34.3	27.6	16.8	13.5

Table 05: Results of ANOVA of feeding (%BW) by silver hake on the Scotian Shelf (1981-1984).

Prey (% BW)	Significance of F						
	Main Effects	Year	Season	Age	Year x Season	Year x Age	Season x Age
All	0.000	0.000	0.001	0.052	0.000	0.000	0.033
Invert.	0.000	0.000	0.354	0.000	0.000	0.000	0.000
Fish	0.000	0.000	0.002	0.035	0.003	0.443	0.148

Table 06: Results of ANOVA for total silver hake consumption (%BW/Day) on the Scotian Shelf (1981-84).

Consumption	Significance of F						
	Main Effects	Year	Season	Age	Year x Season	Year x Age	Season x Age
Total	0.000	0.000	0.000	0.120	0.000	0.014	0.853
Invertebrate	0.000	0.000	0.006	0.048	0.000	0.002	0.750
Fish	0.000	0.184	0.064	0.000	0.364	0.275	0.656

Table 07: Daily consumption of silver hake by age groups for 1981-1986, all seasons.

Age of fish	Season of the Year								
	Winter Mean Consumption/DAY			Spring Mean Consumption/DAY			Summer Mean Consumption/DAY		
	Mean	Standard Deviation	Number of Sets	Mean	Standard Deviation	Number of Sets	Mean	Standard Deviation	Number of Sets
Age 1	8.27	2.63	9	2.29	1.98	41	2.19	3.50	31
Age 2	.73	1.13	10	2.68	2.65	72	2.55	5.05	57
Age 3	1.62	.57	3	2.68	3.32	55	2.13	2.73	45
Age 4	5.59	9.87	4	3.47	4.65	77	2.47	3.76	53
Age 5	.33	.	1	3.60	5.84	61	2.41	5.22	38
Age 6	.	.	.	4.07	8.62	47	2.80	6.44	23
Age 7	.85	.70	3	2.44	6.14	29	3.09	5.72	22
Age 824	.46	5	7.99	10.04	3
Age 915	.29	7	3.00	3.51	6
Age 10+64	.79	6	1.25	1.74	8
Total	3.73	4.91	30	2.97	4.93	400	2.50	4.54	286

Age of fish	Season of the Year (Cont.)					
	Fall			Total		
	Mean	Standard Deviation	Number of Sets	Mean	Standard Deviation	Number of Sets
Age 1	3.81	3.78	33	3.18	3.45	114
Age 2	3.20	3.46	47	2.67	3.71	186
Age 3	3.10	5.45	26	2.55	3.63	129
Age 4	3.15	6.05	46	3.14	4.95	180
Age 5	1.87	3.45	24	2.87	5.26	124
Age 6	1.85	4.14	17	3.30	7.37	87
Age 7	1.33	2.54	12	2.38	5.33	66
Age 8	1.82	2.20	4	2.70	5.51	12
Age 9	.02	.03	2	1.28	2.56	15
Age 10+	2.17	3.05	2	1.14	1.58	16
Total	2.84	4.44	213	2.82	4.70	929

Table 08: Consumption for silver hake

(a) Diet (%BW) of silver hake prey for silver hake at age

Prey Age Groups	Predator Age Group								
	1	2	3	4	5	6	7	8	9
*	1.80	.60	.70	3.90	17.90	24.90	52.70	51.50	54.50

(b) Preference of silver hake prey by silver hake at age

Prey Age Groups	Predator Age Group								
	1	2	3	4	5	6	7	8	9
0*	1.000	.279	.156	.145	.049	.060	.051	.029	.041
1*	.000	.721	.844	.855	.223	.264	.366	.098	.127
2*	.000	.000	.000	.000	.728	.676	.542	.208	.310
3*	.000	.000	.000	.000	.000	.000	.041	.308	.500
4*	.000	.000	.000	.000	.000	.000	.000	.358	.022

(c) Availability of prey to the predator (/year)

Prey Age Groups	Predator Age Group								
	1	2	3	4	5	6	7	8	9
0*	.50	.50	.50	.50	.50	.50	.50	.50	.50
1*	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2*	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
3*	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
4*	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

(d) Average ration (%BW/day) by predators

Prey Age Groups	Predator Age Group								
	1	2	3	4	5	6	7	8	9
*	3.18	2.67	2.55	3.14	2.87	3.30	2.38	2.70	1.28

(e) Percent Body Weight of silver hake consumed by each predator/year

Prey Age Groups	Predator Age Group								
	1	2	3	4	5	6	7	8	9
0*	10.45	.81	.51	3.24	4.57	8.98	11.58	7.41	5.17
1*	.00	4.22	5.50	38.22	41.88	79.14	167.41	49.58	32.37
2*	.00	.00	.00	.00	136.50	202.82	248.26	105.48	78.99
3*	.00	.00	.00	.00	.00	.00	18.98	156.11	127.26
4*	.00	.00	.00	.00	.00	.00	.00	181.55	5.68
0+*	10.45	5.03	6.01	41.46	182.94	290.94	446.23	500.12	249.46

(f) Average Body weight (grams) per predator

Prey Age Groups	Predator Age Group								
	1	2	3	4	5	6	7	8	9
	67	169	213	241	276	331	425	562	732

Outputs

(g) Consumption (grams/year) for silver hake cannibals

Prey Age Groups	Predator Age Group								
	1	2	3	4	5	6	7	8	9
0*	7	1	1	8	13	30	49	42	38
1*	0	7	12	92	116	262	711	279	237
2*	0	0	0	0	377	671	1055	593	578
3*	0	0	0	0	0	0	81	877	932
4*	0	0	0	0	0	0	0	1020	42
0+*	7	9	13	100	505	963	1896	2811	1826

(h) Estimated numbers consumed (EATEN) by silver hake cannibals per year

Prey Age Groups	Predator Age Group								
	1	2	3	4	5	6	7	8	9
0*	.23	.05	.04	.26	.42	.99	1.64	1.39	1.26
1*	.00	.11	.17	1.37	1.73	3.91	10.62	4.16	3.54
2*	.00	.00	.00	.00	2.45	4.36	6.85	3.85	3.75
3*	.06	.00	.00	.00	.00	.41	4.41	4.41	4.68
4*	.00	.00	.00	.00	.00	.00	.00	4.27	.17
0+*	.23	.15	.21	1.63	4.59	9.26	19.52	18.07	13.41

Table 09. Results from the CANCOHORT analysis on silver hake.

CATCH BIOMASS										
Age*	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979
1 *	11238	8784	21242	11077	6373	9721	9673	132	1406	590
2 *	94251	52499	54813	189814	50316	56724	56484	6400	9985	7445
3 *	36113	32901	14951	20905	30751	12839	17815	16430	15611	13812
4 *	13283	18988	11497	26669	2199	14411	8544	8573	9690	11404
5 *	6271	6941	4883	28597	3876	18434	2272	2771	5502	8452
6 *	3893	845	4151	8636	1749	2195	1409	1034	2825	5836
7 *	1696	3017	560	7373	91	352	431	322	1231	2087
8 *	1402	1109	552	4791	126	456	131	607	1000	918
9 *	922	1262	538	568	0	589	335	568	329	637
1+*	169068	126345	113186	298430	95481	115722	97094	36838	47581	51179
2+*	157830	117561	91944	287354	89109	106001	87421	36706	46174	50589
3+*	63579	65062	37132	97539	38793	49277	30937	30306	36189	43145
4+*	27466	32161	22181	76634	8042	36437	13122	13876	20578	29333

Age*	1980	1981	1982	1983	1984	1985	1986
1 *	257	56	1102	180	6251	2947	7681
2 *	8541	2793	7623	11191	5919	27366	10871
3 *	17469	21463	14915	10478	36299	13426	34630
4 *	10049	9556	19167	6975	17863	21964	15782
5 *	4924	4537	11445	3950	5338	6335	8018
6 *	2262	2047	3560	1604	1973	2920	3151
7 *	875	456	1342	445	457	1417	867
8 *	207	73	609	310	105	386	426
9 *	80	48	120	56	2	229	55
1+*	44663	41030	59883	35189	74207	77391	81482
2+*	44406	40974	58781	35009	67956	74444	73801
3+*	35865	38181	51158	23818	62037	47078	62930
4+*	18396	16718	36244	13340	25738	33252	28299

Ag	POPULATION NUMBERS								
	1970	1971	1972	1973	1974	1975	1976	1977	1978
1	2766483	2735418	4689140	2534303	1725303	1855849	1400299	1422039	1530961
2	1829007	1272614	1304328	2684918	796295	969462	944315	624478	711820
3	511143	505364	325052	274320	305524	183261	235831	274924	266628
4	208970	178715	220769	184687	99434	108266	92053	115734	139163
5	54586	85221	63288	131169	28127	71014	27216	39935	60824
6	24593	19646	39084	27832	8557	10840	15962	13673	21053
7	10118	8596	11632	20098	2551	3079	3334	8514	7525
8	8138	3828	1555	6848	1025	1634	1810	1814	5312
9	1872	3828	1475	684	108	598	798	1127	754
1	5414910	4813229	6656323	5864859	2966924	3204003	2721617	2502238	2744039
2	2648427	2077811	1967183	3330557	1241621	1348153	1321318	1080199	1213079
3	819420	805197	662855	645638	445326	378692	377003	455721	501259
4	308277	299834	337803	371318	139802	195431	141172	180797	234631

Age*	1979	1980	1981	1982	1983	1984	1985	1986
1 *	1362846	1022709	1322154	1743945	1530736	3045496	2855333	7218381
2 *	679535	614555	486499	701209	943274	834379	1795216	1425927
3 *	215260	235145	295373	214701	304643	528048	411625	948584
4 *	109974	93444	114236	137653	106486	198246	252501	265020
5 *	54503	38326	41731	56788	46717	59224	91675	119714
6 *	24854	12254	13170	16293	9593	20643	23980	42659
7 *	7082	2771	3155	4286	3615	2803	9423	8740
8 *	2406	589	480	1559	589	1481	1055	3533
9 *	1916	168	113	214	188	6	849	180
1+*	2458375	2019961	2276912	2875649	2945841	4690326	5441657	10032738
2+*	1095529	997252	954758	1132703	1415105	1644830	2586323	2814358
3+*	415994	382697	468259	431494	471831	810452	791108	1388431
4+*	200734	147552	172886	216793	167188	282403	379482	439846

POPULATION BIOMASS AT BEGINNING OF YEAR									
Age*	1970	1971	1972	1973	1974	1975	1976	1977	1978
1 *	113645	112369	108745	93872	45855	74540	63125	58649	71262
2 *	188665	111526	89989	227316	60670	95800	94034	60096	58784
3 *	69215	77780	53166	43980	49370	32446	46050	48468	42642
4 *	38946	36807	46894	42216	25730	23806	23710	30912	30317
5 *	13572	22536	16696	34902	8850	27308	8453	13147	17425
6 *	8243	7254	16371	9653	3412	4611	8010	6266	7609
7 *	3574	4186	5423	10446	1669	2406	2063	5053	3341
8 *	6158	2394	1338	4452	767	1809	2154	1723	3061
9 *	1554	2514	1266	833	3	822	829	1315	693
1+*	443571	377367	339890	467670	196328	263548	248429	225630	235134

Age*	1979	1980	1981	1982	1983	1984	1985	1986
1 *	37669	41033	29026	31016	56111	99676	114316	386792
2 *	59030	56995	37251	51097	80411	74339	177971	157776
3 *	31928	42588	48726	38314	52715	82989	71630	167972
4 *	22706	22113	26255	32532	24924	44571	53919	57561
5 *	13832	10765	12452	16224	13834	15488	24033	30587
6 *	7755	3958	4540	5803	3311	6874	7219	12275
7 *	2604	1172	1565	1805	1420	1136	3681	3168
8 *	1072	293	257	975	330	712	550	1597
9 *	1005	114	78	155	129	4	521	112
1+*	177602	179030	160151	177921	233185	325790	453840	817840

Table 09. Results from the CANCOHORT analysis on silver hake (Cont.)

MEAN POPULATION BIOMASS (KG.)									
Age*	1970	1971	1972	1973	1974	1975	1976	1977	1978
1*	115754	77488	201533	68009	82721	90574	60712	63766	51524
2*	130736	89691	79553	143099	54407	81240	80897	62024	45998
3*	53118	64815	51959	37414	38995	32257	41599	41960	30895
4*	30748	28393	41346	21145	26180	14044	17094	24797	20499
5*	10432	18702	11870	13955	7221	17896	8024	11727	11429
6*	6194	6885	15929	4843	2909	2938	6266	5318	4254
7*	3060	2472	4364	3296	2007	2708	2095	4529	1731
8*	4040	2065	1344	1551	916	1470	1804	1306	1670
9*	855	1361	837	387	0	535	415	758	338
1+*	354937	291873	408736	293698	215357	243662	218907	216184	168336
2+*	239183	214386	207203	225689	132635	153088	158194	152418	116812
3+*	108448	124694	127650	82590	78229	71848	77297	90395	70814
4+*	55329	59879	75691	45177	39233	39591	35698	48435	39920
Age*	1979	1980	1981	1982	1983	1984	1985	1986	
1*	57483	29665	35307	72945	62063	149188	158851	365747	
2*	64850	61577	47666	70396	93168	88149	207403	153011	
3*	29292	35757	39976	34443	50302	71138	68633	153402	
4*	16744	18017	20428	24495	19845	34501	42811	45092	
5*	8207	7642	8649	8951	9709	10891	17736	22908	
6*	3590	2489	2946	3418	2020	5253	4955	9003	
7*	1122	696	1525	923	930	817	2519	2478	
8*	459	177	182	390	91	679	304	1218	
9*	581	87	52	112	100	3	339	72	
1+*	182330	156107	156731	216073	238227	360619	503551	752932	
2+*	124846	126442	121424	143128	176164	211431	344701	387185	
3+*	59997	64865	73758	72732	82996	123282	137297	234173	
4+*	30705	29108	33782	38289	32694	52143	68664	80771	

MEAN WEIGHT OF INDIVIDUALS IN CATCH

*	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984
*	.14	.14	.11	.14	.14	.17	.15	.22	.17	.22	.21	.21	.24	.19	.17
* 1985 1986															
*	.19	.17													

MEAN AGE OF INDIVIDUALS IN CATCH

*	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981
*	2.23	2.25	1.88	2.26	2.16	2.26	2.02	3.06	2.95	3.55	3.10	3.34
* 1982 1983 1984 1985 1986												
*	3.35	2.91	2.75	2.83	2.70							

WEIGHTS AT THE BEGINNING OF THE YEAR

Age*	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
1*	.04	.04	.02	.04	.03	.04	.05	.04	.05	.03	.04	.02	.02
2*	.10	.09	.07	.08	.08	.10	.10	.10	.08	.09	.09	.08	.07
3*	.14	.15	.16	.16	.16	.18	.20	.18	.16	.15	.18	.16	.14
4*	.19	.21	.21	.23	.26	.22	.26	.27	.22	.21	.24	.23	.24
5*	.25	.26	.26	.27	.31	.38	.31	.33	.29	.25	.28	.30	.29
6*	.34	.37	.42	.35	.40	.43	.50	.46	.36	.31	.32	.34	.36
7*	.35	.49	.47	.52	.65	.78	.62	.59	.44	.37	.42	.50	.42
8*	.76	.63	.86	.65	.75	1.11	1.19	.95	.58	.45	.50	.53	.63
9*	.83	.66	.86	1.22	.03	1.37	1.04	1.17	.92	.52	.68	.69	.72
Age*	1983	1984	1985	1986	1987								
1*	.04	.03	.04	.05	.00								
2*	.09	.09	.10	.11	.07								
3*	.17	.16	.17	.18	.23								
4*	.23	.22	.21	.22	.23								
5*	.30	.26	.26	.26	.24								
6*	.35	.33	.30	.29	.29								
7*	.39	.41	.39	.36	.31								
8*	.56	.48	.52	.45	.45								
9*	.69	.70	.61	.62	.53								

FISHING MORTALITY

Age*	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
1*	.097	.114	.106	.164	.077	.108	.160	.002	.027	.010	.009
2*	.727	.591	.697	1.355	.935	.705	.704	.104	.219	.115	.139
3*	.684	.509	.288	.562	.793	.399	.429	.392	.507	.473	.490
4*	.434	.672	.278	1.282	.084	1.036	.501	.346	.475	.685	.559
5*	.605	.372	.413	2.158	.540	1.048	.284	.237	.484	1.048	.649
6*	.633	.123	.261	1.859	.605	.755	.225	.195	.670	1.685	.921
7*	.558	1.248	.128	2.372	.045	.130	.206	.071	.718	1.945	1.287
8*	.348	.540	.412	3.374	.138	.311	.073	.467	.603	2.100	1.193
9*	.937	.806	.567	1.298	.847	.955	.705	.657	.846	.951	.801
3+*	.609	.531	.293	1.235	.609	.711	.425	.356	.507	.713	.544
Age*	1981	1982	1983	1984	1985	1986					
1*	.002	.015	.003	.042	.019	.021					
2*	.059	.109	.120	.067	.132	.071					
3*	.538	.434	.208	.512	.202	.226					
4*	.469	.787	.352	.519	.514	.350					
5*	.527	1.310	.408	.493	.358	.350					
6*	.701	1.060	.803	.377	.593	.350					
7*	.300	1.498	.481	.562	.566	.350					
8*	.401	1.616	3.781	.155	1.301	.350					
9*	.807	.933	.496	.783	.596	.663					
3+*	.523	.701	.279	.508	.338	.265					

Table 09. Results from the CANCOHORT analysis on silver hake (Cont.)

FINAL CANNIBALISM MORTALITY

Age*	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981
1 *	.473	.421	.249	.777	.296	.364	.441	.485	.578	.579	.529	.429
2 *	.339	.550	.630	.556	.307	.483	.311	.540	.760	.732	.388	.552
3 *	.154	.111	.074	.241	.032	.085	.077	.084	.170	.154	.027	.019
4 *	.254	.153	.040	.353	.052	.121	.126	.093	.253	.156	.040	.025
5 *	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
6 *	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
7 *	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
8 *	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
9 *	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000

Age*	1982	1983	1984	1985	1986
1 *	.396	.401	.284	.471	.197
2 *	.517	.257	.434	.302	.575
3 *	.062	.020	.021	.037	.026
4 *	.080	.032	.046	.026	.077
5 *	.000	.000	.000	.000	.000
6 *	.000	.000	.000	.000	.000
7 *	.000	.000	.000	.000	.000
8 *	.000	.000	.000	.000	.000
9 *	.000	.000	.000	.000	.000

FINAL NATURAL MORTALITY (CANNIBALISM AND RESIDUAL MORTALITY)

Age*	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981
1 *	.673	.621	.449	.977	.496	.564	.641	.685	.778	.779	.729	.629
2 *	.539	.750	.830	.756	.507	.683	.511	.740	.960	.932	.588	.752
3 *	.354	.311	.274	.441	.232	.285	.277	.284	.370	.354	.227	.219
4 *	.454	.353	.240	.553	.252	.321	.326	.293	.453	.356	.240	.225
5 *	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400
6 *	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400
7 *	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400
8 *	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400
9 *	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400	.400

Age*	1982	1983	1984	1985	1986
1 *	.596	.601	.484	.671	.397
2 *	.717	.457	.634	.502	.775
3 *	.262	.220	.221	.237	.226
4 *	.280	.232	.246	.226	.277
5 *	.400	.400	.400	.400	.400
6 *	.400	.400	.400	.400	.400
7 *	.400	.400	.400	.400	.400
8 *	.400	.400	.400	.400	.400
9 *	.400	.400	.400	.400	.400

NEW TOTAL MORTALITY

Age*	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
1 *	.777	.741	.558	1.158	.576	.676	.808	.692	.812	.796	.743
2 *	1.286	1.365	1.559	2.173	1.469	1.414	1.234	.851	1.196	1.061	.733
3 *	1.051	.828	.565	1.015	1.037	.689	.712	.681	.886	.834	.722
4 *	.897	1.038	.521	1.882	.337	1.381	.835	.643	.937	1.054	.806
5 *	1.022	.780	.822	2.730	.954	1.493	.688	.640	.895	1.492	1.068
6 *	1.051	.524	.665	2.390	1.022	1.179	.628	.597	1.089	2.194	1.357
7 *	.972	1.710	.530	2.976	.446	.532	.609	.472	1.140	2.487	1.752
8 *	.754	.954	.821	4.153	.539	.717	.474	.878	1.020	2.663	1.650
9 *	.988	.867	.680	1.367	.904	1.006	.782	.745	.903	1.002	.863

Age*	1981	1982	1983	1984	1985	1986
1 *	.634	.615	.607	.529	.694	.418
2 *	.818	.834	.580	.707	.638	.846
3 *	.764	.701	.430	.738	.440	.452
4 *	.699	1.081	.587	.771	.746	.627
5 *	.940	1.778	.817	.904	.765	.750
6 *	1.123	1.506	1.230	.784	1.009	.750
7 *	.705	1.985	.892	.977	.981	.750
8 *	.809	2.116	4.641	.557	1.768	.750
9 *	.868	.985	.632	.848	.700	.750

DISTRIBUTION OF GROWTH OVER AGES (PER CENT)

Age*	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980
1 *	47.4	24.8	67.1	22.1	54.5	47.3	37.6	46.7	44.4	46.3	25.3
2 *	29.9	44.3	22.1	60.0	28.2	37.3	43.5	37.1	41.7	37.0	50.8
3 *	12.4	15.9	5.3	9.5	8.1	7.9	11.8	10.9	10.9	10.3	13.0
4 *	6.0	6.4	2.8	2.6	5.8	2.2	3.0	2.6	3.9	4.0	6.6
5 *	2.3	5.9	.8	1.6	1.4	3.9	2.7	2.1	.7	1.5	2.5
6 *	1.3	1.3	1.3	1.4	1.1	.5	.8	.3	2.6	.6	1.3
7 *	1.0	.9	.4	2.4	.6	.7	.8	.2	2.5	.2	.4
8 *	2.3	.6	.2	.5	.3	.0	.0	.1	2.6	.1	.1
9 *	.1	2.1	.0	2.8	.0	.2	2.1	.1	.0	.1	.1

Age*	1981	1982	1983	1984	1985	1986
1 *	42.2	53.6	43.2	63.2	50.6	40.1
2 *	37.9	34.2	43.7	23.9	40.2	41.8
3 *	13.5	6.1	10.4	9.3	5.3	14.6
4 *	4.0	4.3	1.7	2.4	2.8	1.8
5 *	1.3	1.3	.7	.6	.6	1.1
6 *	.5	.3	.2	.4	.3	.3
7 *	.5	.2	.1	.1	.1	.2
8 *	.0	.0	.0	.1	.0	.1
9 *	.0	.0	.0	.0	.0	.0

Table 10a:Thompson and Bell Yield per Recruit analysis (no cannibalism).

INPUTS

Age	Weight-At-Age	Partial Recruitment
1	.067	.080
2	.154	.580
3	.199	1.000
4	.239	1.000
5	.275	1.000
6	.331	1.000
7	.425	1.000
8	.562	1.000
9	.678	1.000

Natural Mortality Rate : 0.4
 F0.1 Computed As .5327 At Y/R Of .0651

OUTPUTS

Fishing Mortality	Catch (Number)	Yield (Kg)	Avg. Weight (Kg)	Yield Per Unit Effort
.1000	.119	.027	.226	2.203
.2000	.202	.043	.212	1.751
.3000	.263	.053	.201	1.438
.4000	.310	.059	.192	1.213
.5000	.346	.064	.185	1.046
F0.1---.5327	.357	.065	.183	1.000
.6000	.377	.067	.179	.917
.7000	.402	.070	.174	.816
.8000	.423	.072	.170	.734
.9000	.442	.073	.166	.667
1.0000	.458	.075	.163	.611
1.1000	.473	.076	.160	.563
1.2000	.486	.077	.158	.522
1.3000	.498	.077	.156	.487
1.4000	.508	.078	.153	.456
1.5000	.518	.079	.152	.428
FMAX---3.1205	.515	.081	.132	.213

Table 10b:Thompson and Bell Yield per Recruit analysis with cannibalism.

INPUTS

Age	Weight-At-Age	Partial Recruitment	Natural Mortality
1	.058	.060	.733
2	.147	.203	.642
3	.203	.645	.236
4	.250	1.000	.247
5	.296	1.000	.400
6	.354	1.000	.400
7	.469	1.000	.400
8	.579	1.000	.400
9	.764	1.000	.400

F0.1 Computed As .4366 At Y/R Of .0415
 Fmax Computed As 5.6652 At Y/R Of .0534

OUTPUTS

Yield Per Recruit Analysis

Fishing Mortality	Catch (Number)	Yield (Kg)	Avg. Weight (Kg)	Yield Per Unit Effort
.1000	.082	.020	.238	2.052
.2000	.138	.030	.220	1.595
.3000	.178	.037	.206	1.284
.4000	.208	.040	.194	1.064
F0.1---4.666	.218	.042	.190	1.000
.5000	.233	.043	.185	.904
.6000	.252	.045	.177	.783
.7000	.269	.046	.171	.690
.8000	.283	.047	.165	.616
.9000	.296	.048	.160	.556
1.0000	.308	.048	.156	.506
1.1000	.318	.049	.153	.465
1.2000	.328	.049	.150	.430
1.3000	.337	.049	.147	.400
1.4000	.345	.050	.144	.373
1.5000	.353	.050	.142	.350
FMAX---5.6652	.522	.053	.102	.099

Table 11 Summary of Projections without and with cannibalism included.

A: Inputs to projections

Age	Catch	Mean Wtgs	1986 Population Numbers ('000) without Cannibalism	Partial Recruitment	Average Recruitment ('000)	Quota 1987 (0) 1988 (0) F _{0.1}	1986 Population Numbers ('000) including Cannibalism	Partial recruitment	Average Recruitment ('000)	Quota 1987 (0) 1988 (0) F _{0.1}	Average Natural Mortality (Cannibalism)
1	123882	.055	5438504	.08	992097	85000	7218381	0.060	1654967	85000	.661
2	68374	.142	448513	.58		12000	1425927	0.203		120000	.698
3	172291	.201	699719	1.00		.53	948584	0.645		.44	.266
4	68918	.257	279894	1.00			265020	1.000			.283
5	29477	.310	119714	1.00			119714	1.000			.400
6	10504	.375	42659	1.00			42659	1.000			.400
7	2152	.488	8740	1.00			8740	1.000			.400
8	870	.631	3533	1.00			3533	1.000			.400
9	84	.806	341	1.00			180	1.000			.400

B: Projections

Scenario 1: Projections with cannibalism

Production

Source	1986	1987	1988	1989	1990
Recruitment Biomass	250252	57376	57376	57376	57376
Growth	430468	372472	242883	205392	180569
Total Production	680720	429848	300259	262767	237944
Loss Through Fishing	83704	85000	120000	161550	118065
Surplus Production	319529	48780	57155	44320	41528
Net Production	235825	-36220	-62845	-117231	-76537

Production/Biomass Ratio

1986	1987	1988	1989	1990
1.01	.61	.49	.51	.57

Summary Of Projections

Year	1986	1987	1988	1989	1990
Population Numbers	10032738	6756829	5085386	4422477	3817401
Population Biomass	673818	708636	618962	519610	418885
Catch	83703	85000	120000	161550	118065
F Or Quota	83703	85000	120000	.44	.44

Age Groups Considered: 1+

Scenario 2: Without Cannibalism

Production

Source	1986	1987	1988	1989	1990
Recruitment Biomass	188546	34395	34395	34395	34395
Growth	312880	325113	205308	157051	127707
Total Production	501426	359508	239703	191445	162102
Loss Through Fishing	83704	85000	120000	174062	117104
Surplus Production	307514	122643	-29518	32611	46488
Net Production	223810	37643	-90482	-141451	-70617

Production/Biomass Ratio

1986	1987	1988	1989	1990
1.03	.61	.46	.48	.56

Summary Of Projections

Year	1986	1987	1988	1989	1990
Population Numbers	7041530	5327621	4161937	3313091	2607118
Population Biomass	484780	592164	525462	397087	289035
Catch	83704	85000	120000	174062	117105
F Or Quota	83704	85000	120000	0.53	0.53

Age Groups Considered: 1+

Scenario 3: Cannibalism mortality included in Natural mortality. All other inputs similar to scenario 2.

Production

Source	1986	1987	1988	1989	1990
Recruitment Biomass	250252	57376	57376	57376	57376
Growth	430468	372472	242883	202733	174208
Total Production	680720	429848	300259	260109	231584
Loss Through Fishing	83704	85000	120000	188955	128915
Surplus Production	319529	48780	57155	46673	46392
Net Production	235825	-36220	-62845	-142282	-82523

Production/Biomass Ratio

1986	1987	1988	1989	1990
1.01	.61	.49	.52	.59

Summary Of Projections

Year	1986	1987	1988	1989	1990
Population Numbers	10032738	6756829	5085387	4422478	3728004
Population Biomass	673819	708636	618962	504837	389703
Catch	83704	85000	120000	188955	128915
F Or Quota	83704	85000	120000	.53	.53

Age Groups Considered: 1+

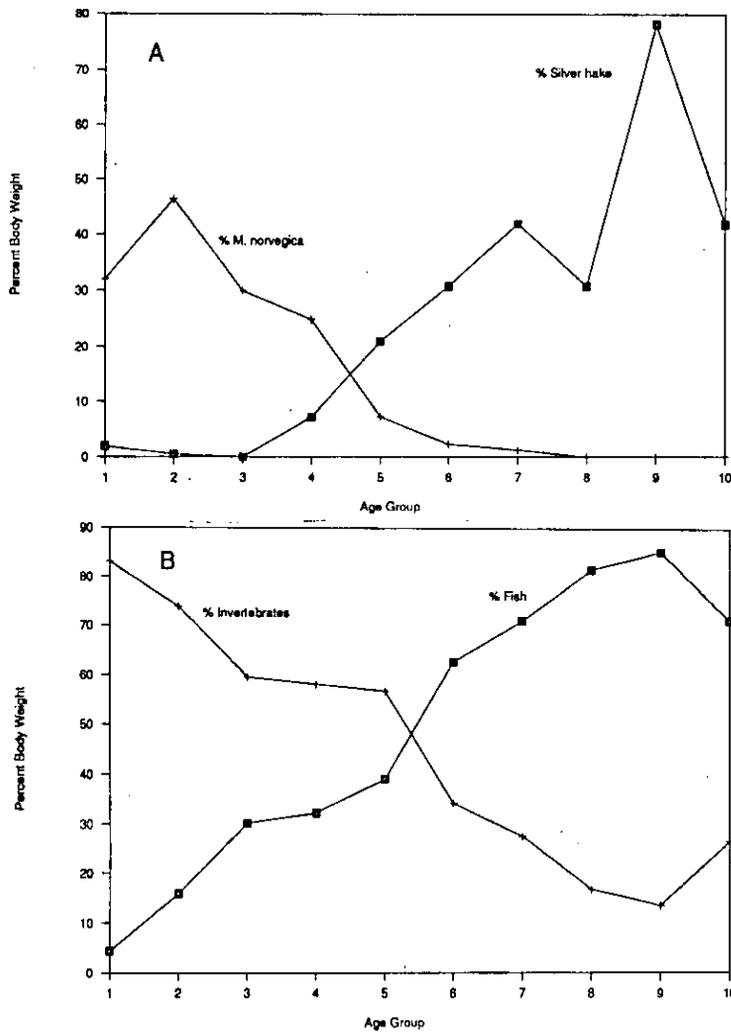


Figure 01: Percent body weight of various prey species found in the guts of silver hake on the Scotian Shelf.

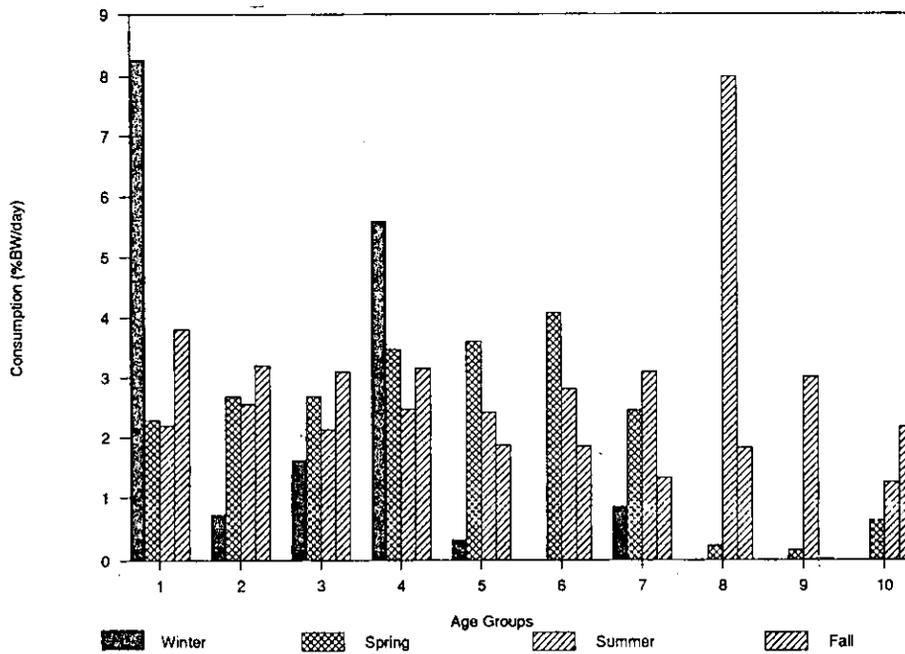


Figure 02: Silver hake consumption rates by season and age.

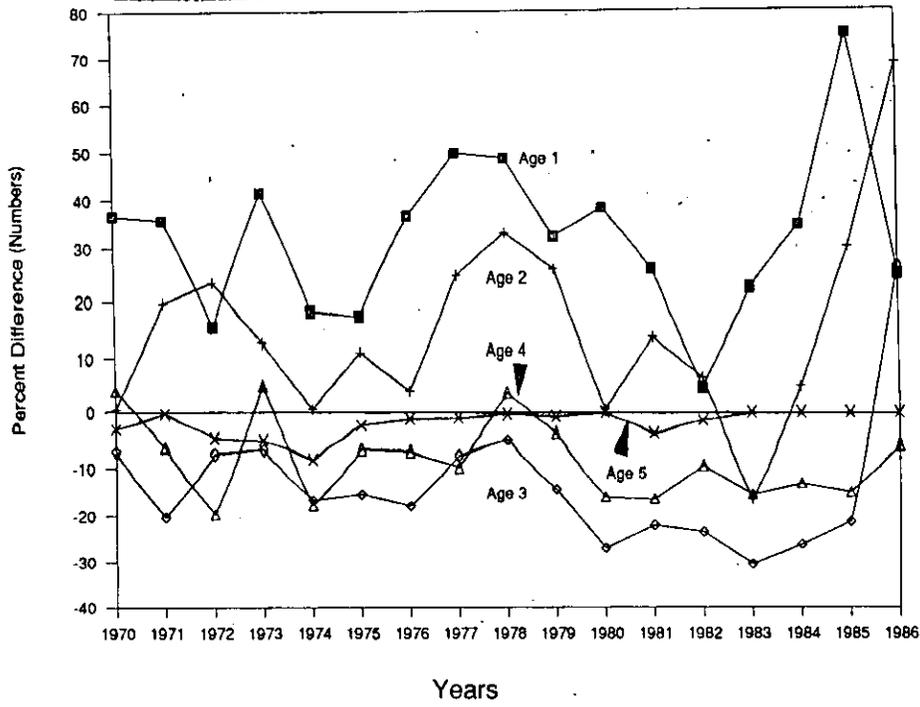


Figure 03: Percent differences in population numbers at age estimated by cohort analysis with and without cannibalism. (CANCOHORT - COHORT)

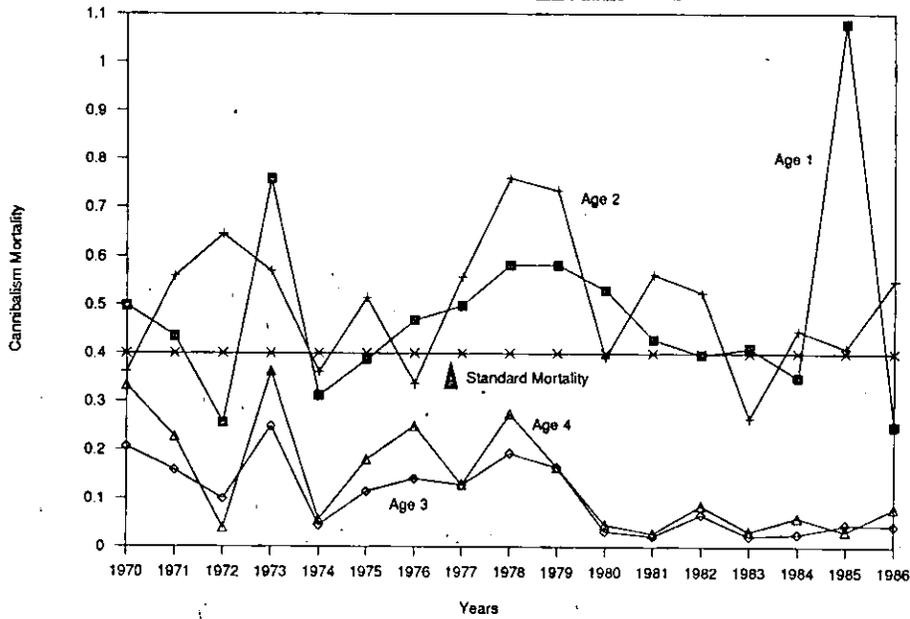


Figure 04. Cannibalism mortality at age for 4VWX silver hake.

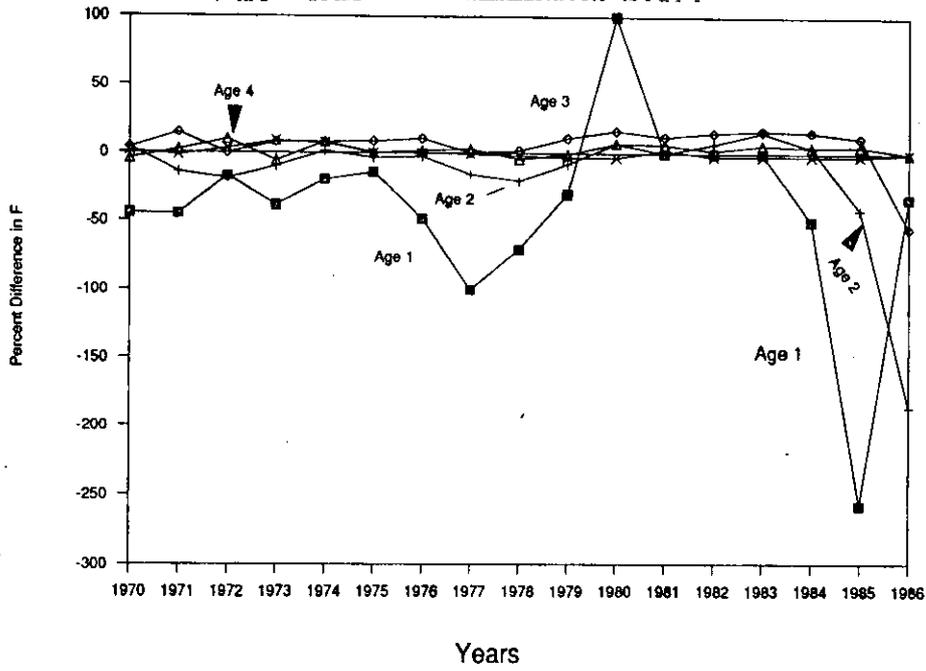


Figure 05. Percent differences in fishing mortality at age for silver hake. (CANCOHORT - COHORT)

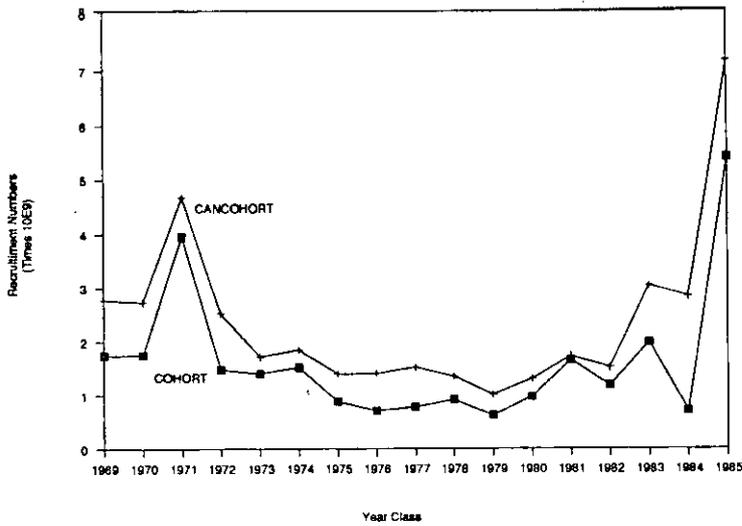


Figure 06. Recruitment from CANCOHORT and COHORT model.

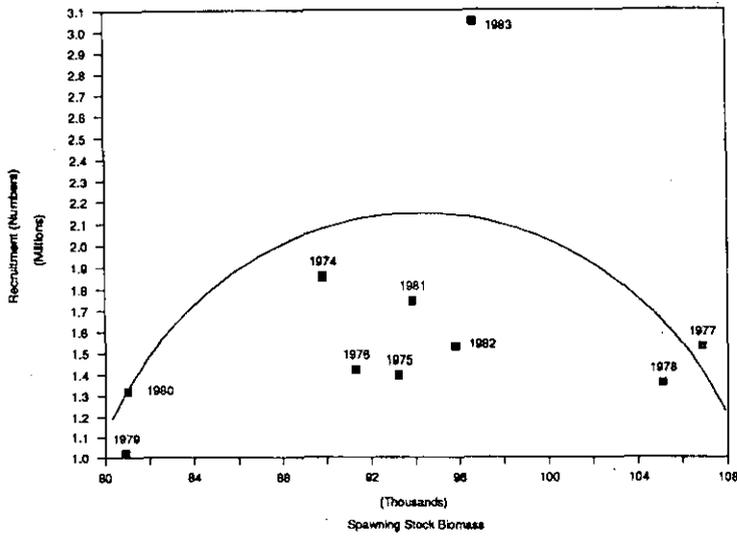


Figure 07. Stock Recruitment relationship from CANCOHORT model. (Curve fitted by eye).

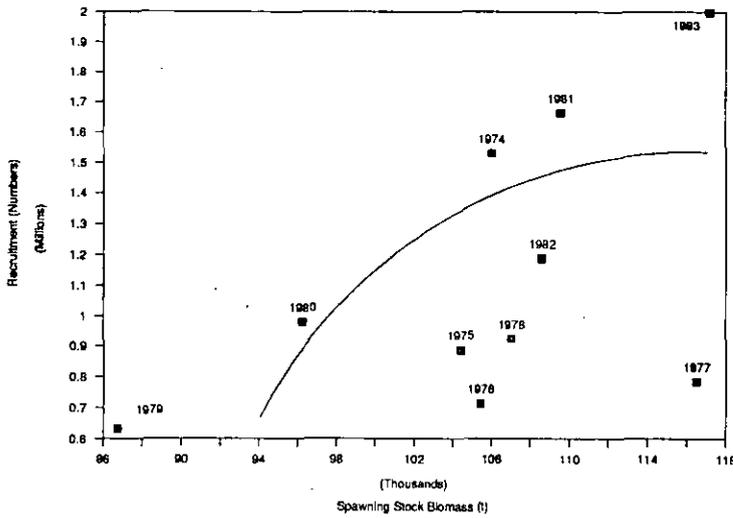


Figure 08. Stock Recruitment relationship from COHORT model. (Curve fitted by eye).

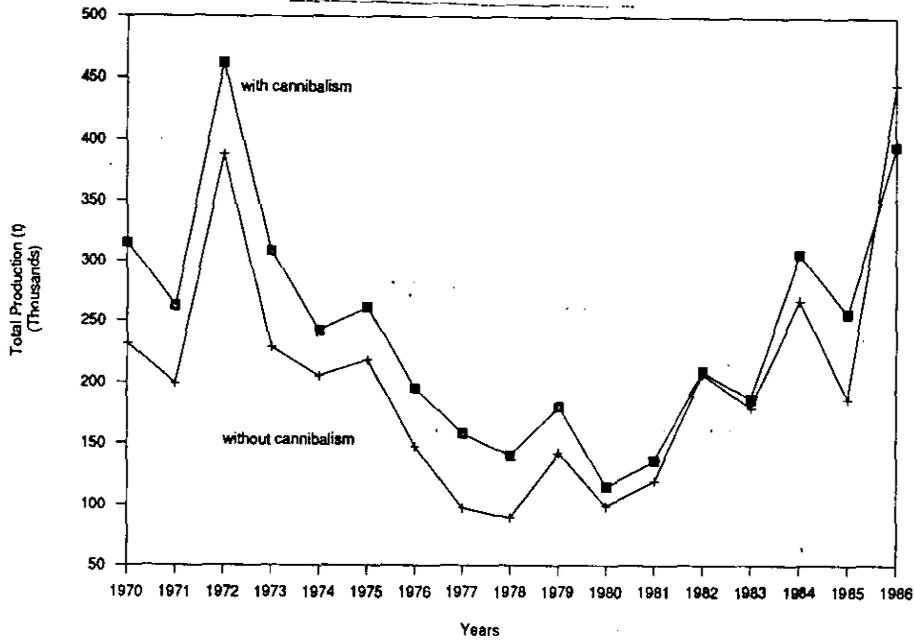


Figure 09. Total Production for the 4VWX silver hake stock from the COHORT and CANCOHORT models.

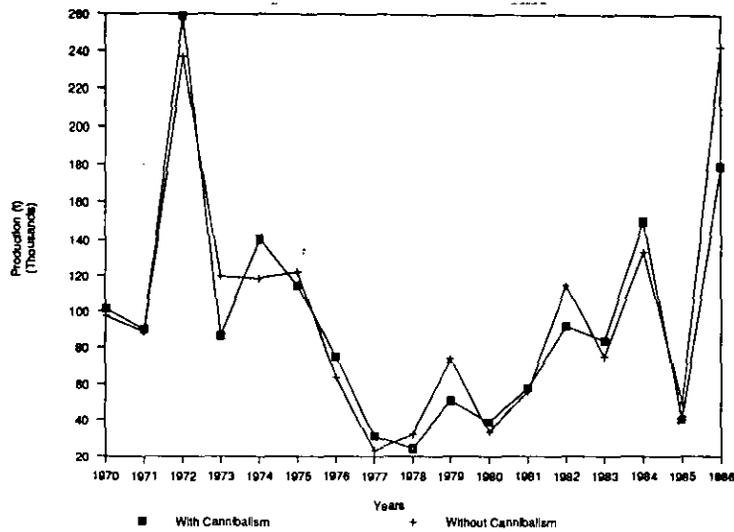


Figure 10: Surplus Production (t) for silver hake.

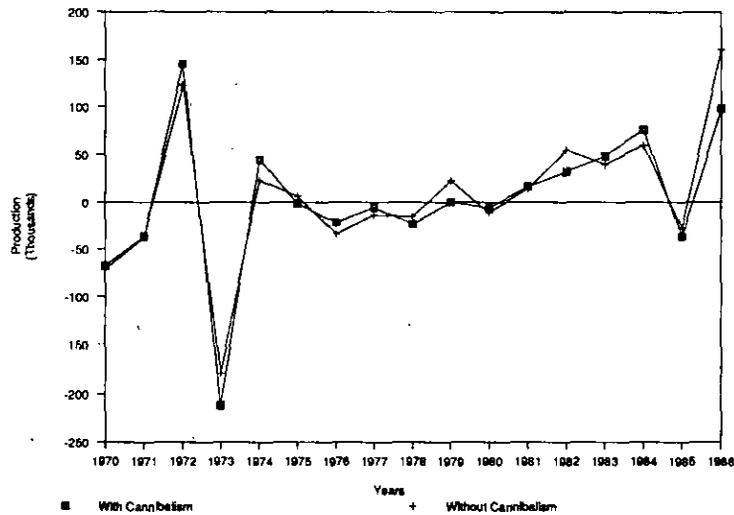


Figure 11: Net Production (t) for silver hake.

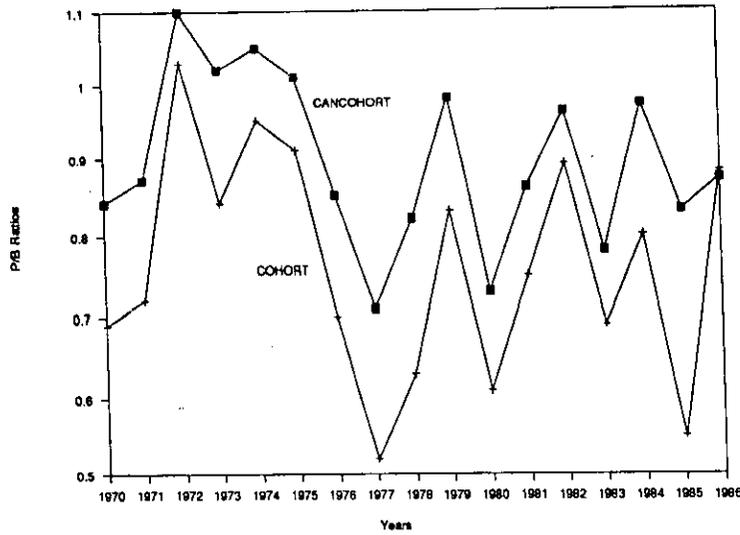


Figure 12: Production Biomass (P/B) ratios for the 4VWX silver hake stock from the COHORT and CANCOHORT models.

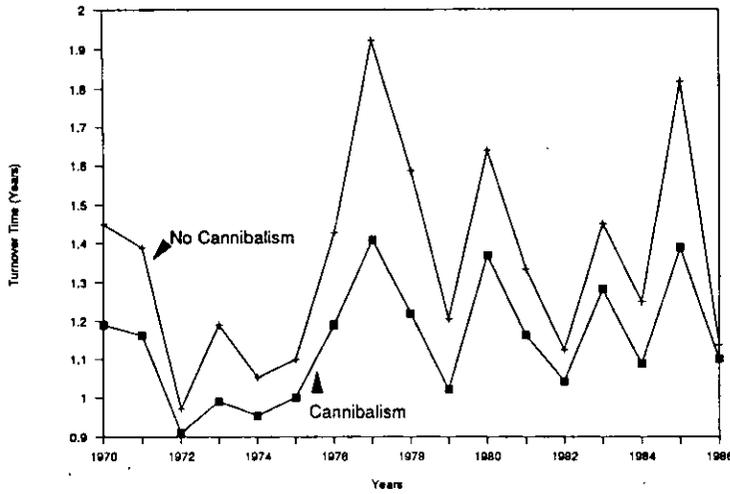


Figure 13: Turnover ($1/(P/B)$) for the 4VWX silver hake stock from the COHORT and CANCOHORT models.

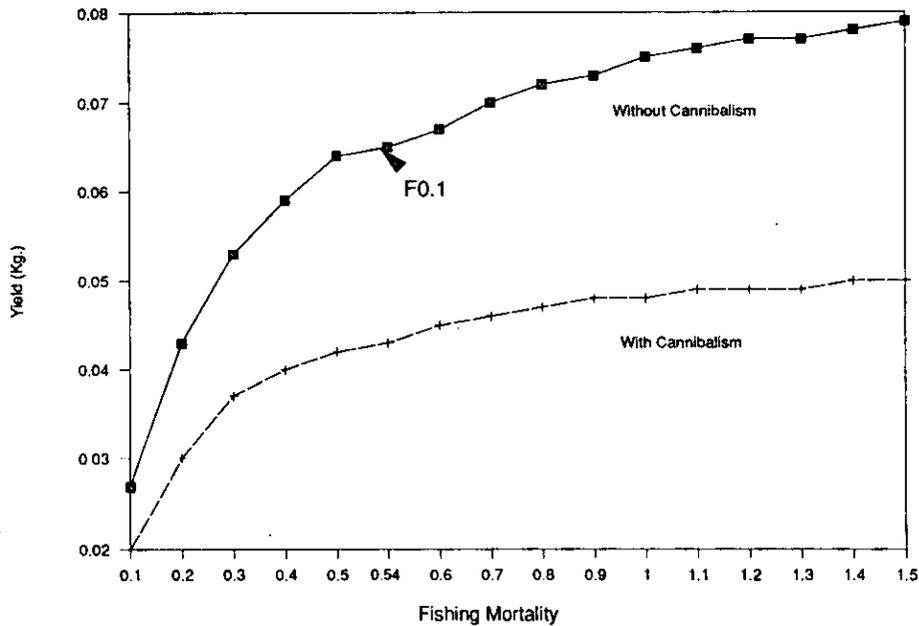


Figure 14. Thompson and Bell Yield per recruit model for cannibalism and no cannibalism.