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Spatial, Temporal and Predator-Prey Size Patterns of Cannibalism by Silver Hake.

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Abstract

Silver Hake (*Merluccius bilinearis*) is an important piscivore in Northwest Atlantic fish community dynamics. This species is known to exert significant predation pressure on other fish populations in this region. Intraspecific predation has been shown in previous studies to account for a substantial component of the diet of this species. The objective of the present study is to document the relative importance of cannibalism in the diet of silver hake in two populations off the northeastern United States during 1981-90 and to examine the role of size-related and spatial processes in the occurrence and importance of intraspecific predation. Stomach samples for selected species have been routinely collected in conjunction with standardized research vessel surveys off the northeastern United States during spring and autumn. The stomach samples are collected according to a stratified cluster sample design.

Cannibalism represented an important fraction of the diet of silver hake for both populations and seasonal periods. We noted a general trend for increasing cannibalism with increasing size; however evidence for intracohort cannibalism was also found. The occurrence of cannibalism was highly localized, predominately in regions of high overlap between small ($\leq$ 20 cm) and larger ($>$ 20 cm) silver hake and in areas adjacent to high overlap sites. The prevalence of intraspecific predation in this species and the spatial dynamics of this process has important implications for both population regulation and the form of the stock recruitment relationship.

Introduction

Intraspecific predation is an important regulatory mechanism in the dynamics of many invertebrate and vertebrate species (Fox 1975; Polis 1981). Cannibalism has been documented in a diverse array of fish species (Dominey and Blumer 1984; Smith and Reay 1991; Fitzgerald and Whorisky 1992) and its implications for population stability have been appreciated since the classical studies of Ricker (1954). Predation by the parental stock on their progeny is one of several possible mechanisms leading to the Ricker stock-recruitment relationship. This model exhibits a complex range of dynamical behavior including periodic and chaotic population trajectories (Ricker 1954; e.g. May 1976). Invoking cannibalism as an underlying mechanism in the Ricker model, however, involves an implicit assumption of a random encounter between predator and prey. A principal goal of the present study is to examine this assumption.

The importance of intraspecific predation to the diet of silver hake has been shown in several studies (Edwards and Bowman 1979; Waldron 1992) where it has been estimated that up to 25% of the prey can be comprised of conspecifics. It is clear that cannibalism has the potential to contribute strongly to population regulation in this species. The objective of the present study is to examine spatial, temporal and size-related patterns of cannibalism in silver hake, *Merluccius bilinearis*, off the northeastern United States to examine its potential importance in population regulation and in the form of the stock-recruitment relationship.

Materials and Methods

Silver Hake Diet

Standardized research vessel surveys have been conducted on the continental shelf off the northeastern United States by the Northeast Fisheries Science Center in autumn since 1963; spring surveys were initiated in 1968. Winter and summer surveys have been undertaken on a less regular basis. Diet composition has been examined for selected species during the surveys according to several sampling protocols during this period. In the following analyses, we will concentrate on the most recent time period and sampling protocol (1981-present). Stomach contents of selected species, including silver hake, were examined at sea; volumetric estimates of total food contained in the gut were made, and the relative contribution of prey to the lowest possible taxon was estimated. Two populations of silver hake are recognized within the study area: a Northern population in the Gulf of Maine and the northeast peak of Georges Bank and a Southern population on southern Georges Bank to the Middle Atlantic region. Diet composition was determined separately for each population and season.

Stomach samples were collected according to a stratified cluster sample design with each individual haul comprising a cluster; the stratification variables included predator size, region and time of day. For the purposes of the present analysis, samples were pooled over diel periods. The mean stomach content weight (or volume) is given by:

$$\overline{sw}_{il}=\frac{\sum_{j=1}^{m_{ij}} M_{ij}\overline{sw}_{ijl}}{\sum_{j=1}^{n_i} M_{ij}}$$

where

$$\overline{sw}_{ijl}=\frac{\sum_{q=1}^{m_{ij}} sw_{ijlq}}{m_{ij}}$$

and M_{ij} is the number of predators in tow j, stratum i ($j = 1,2,..n_i$); m_{ij} is the number of predators in food habits sample tow j stratum i ($m_{ij} \leq M_{ij}$); n_i is the number of tows with predators in stratum i; and sw_{ijlq} is the stomach content weight or volume of predator stomach q ($q = 1,2,...m_{ij}$), prey species category l, tow j, predator stratum i. The variance of the mean stomach content is:

$$V(\overline{sw}_{il}) \approx \frac{1}{n_i\overline{M}_i^2}\frac{\sum_{j=1}^{n_i} M_{ij}^2(\overline{sw}_{ijl}-\overline{sw}_{il})^2}{n_i-1}$$

where

$$\overline{M}_i=\frac{\sum_{j=1}^{n_i} M_{ij}}{n_i}$$

The coefficient of variation is then:

$$CV(\overline{sw}_{il})=\frac{\{V(\overline{sw}_{il})\}^{1/2}}{\overline{sw}_{il}}$$

Spatial Distribution

We considered the spatial distribution of small (< 20 cm FL) and large (>20 cm FL) silver hake and the incidence of cannibalism by season to examine the role of spatial dynamics in cannibalistic interactions. Tows with fewer than two silver hake stomachs examined were not included in the analysis. Contours of distribution patterns for these two size classes and for the incidence of cannibalism were constructed to examine the overlap is distribution of potential cannibals with respect to potential conspecific prey.

Results and Discussion

Intraspecific predation accounted for a substantial component of the diet of silver hake during 1981-90 (Table 1). These observations are consistent with previous estimates of the relative importance of conspecifics in the diet of silver hake (Langton and Bowman 1980; Bowman 1984; Bowman and Michaels 1984; Waldron 1992). The relative contribution of cannibalism to the diet generally increased with increasing predator size although the relative importance of cannibalism was high in the < 20 cm FL size class for the southern region in autumn. Sample sizes were highest for the intermediate size class (20-40 cm FL) and these estimates are considered the most representative and anomalies for other size classes may reflect sample size limitations. Coefficients of variation based on the cluster sample estimators were relatively high, possibly reflecting the relatively high degree of intra-cluster correlation in these samples and aggregation of the samples over a broad time period and large sample areas. A substantial fraction of the diet of silver hake was comprised of fish prey (Figure 1), consistent with previous studies showing this species to be a dominant piscivore (Edwards and Bowman 1979; Waldron 1992). Fish prey which could not be identified because of advanced state of digestion made up a significant part of the diet and it is likely that silver hake as prey were represented in this component. Decapod crustaceans, euphausids, and cephalopods (squid) were consistently represented in the diet in both regions and seasonal periods.

During spring, large catches of juveniles occurred along the northern slope of Georges Bank and in the Gulf of Maine (Figure 2). In contrast, the spring distribution of larger hake extended farther south along the southern slope of Georges Bank and along the shelf break to Cape Hatteras (Figure 2). Juvenile silver hake were concentrated in the inshore Middle Atlantic region, Cape Cod Bay, and on Georges Bank during the fall (Figure 2). Concentrations of larger (> 20 cm) silver hake were wide-spread throughout the Gulf of Maine and along the Northern slope of Georges Banks, but were also present near the shelf break in the Middle Atlantic region during fall (Figure 2).

The occurrence of cannibalism (percentage of silver hake with conspecifics in the diet) was concentrated in relatively few locations (Figure 3). Consideration of the relative occurrence of cannibalism with respect to distribution patterns of juvenile and larger silver hake indicates that most cannibalism occurs in areas where high abundances of juveniles and adults overlap or in areas between adjacent centers of juvenile and adult abundances. Juveniles may be exposed to cannibalism primarily during migration to adult distribution centers, particularly in the southern population where adult and juvenile distributions are more disjunct.

Examination of the number of silver hake consumed by individual predators in stomach samples in which prey counts could be made indicates that most cannibalistic silver hake consumed a single conspecific; however up to 9 individual silver hake were identified in the stomach of one predator (Figure 4).

Silver hake preyed on conspecifics ranging from 0.8-30 cm FL, and averaging 10.2 cm FL (N=300, Fig. 5). Prey averaged 9 cm FL during the fall and 14 cm during the spring (Fig. 5). An average predator prey size ratio of 4.3 (minimum=1.4, maximum=38). Clearly, larger members of the population had a greater probability of preying on conspecifics. During the fall 25-30 cm cannibals fed on 5-10 cm prey, while during the spring 30-40 cm cannibals fed on 10-15 cm prey. It is also clear that some silver hake exhibit intra-cohort cannibalism with 5-15 cm fishes preying on smaller member of the cohort.

Implications for the Form of the Stock-Recruitment Relationship

The observed patchiness in cannibalism has important implications for the form of the stock recruitment relationship. Consideration of spatial heterogeneity in models of intraspecific predation is therefore warranted. MacCall (1989) describes an extension of the Ricker model which is useful in this context. The generalized model can be written:

$$R=\alpha P e^{-\beta P^{\gamma}}$$

where α and β are represent density-independent and compensatory factors respectively and γ is a parameter controlling the shape of the curve. For the case $\gamma=1$, the classical Ricker model is obtained. However, for the case $0 < \gamma < 1$, which can be expected for a spatially heterogeneous system, the relationship is less peaked (Figure 6). In addition, the slope of the curve at low stock sizes increases. The resilience of the population to harvesting or other disturbances in directly related to the slope of the recruitment curve at the origin and consideration of spatial dynamics therefore is critically important in determining the probable response of the population to stress. In addition, the flatter descending limb of the curve under spatial heterogeneity has important consequences for the dynamic behavior of the model including the occurrence of cyclic and chaotic dynamics. These considerations suggest that detecting spatial patterns of intraspecific predation is critical to understanding the full implications of cannibalism in exploited fish populations.

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Table 1. Estimates of mean stomach content volume (cc) of silver hake as prey, coefficient of variation, percentage contribution to the diet, and number of silver hake stomachs sampled during spring and autumn for the northern and southern populations of silver hake. Size is the upper limit of the length category (cm FL).

	Spring				Autumn			
Size	Mean	C.V.	Percent	N	Mean	C.V.	Percent	N
				Northern Population				
20	0	--	--	828	0.034	0.540	7.2	416
40	0.218	0.330	14.9	1349	0.471	0.453	15.2	3405
60	6.418	0.432	31.4	50	5.323	0.478	17.3	118
				Southern Population				
20	0.057	--[1]	1.0	594	0.580	0.651	66.7	130
40	1.148	0.907	38.1	3105	0.078	0.437	4.2	2094
60	3.870	0.537	19.9	131	2.931	0.732	13.8	29

[1] Not estimable

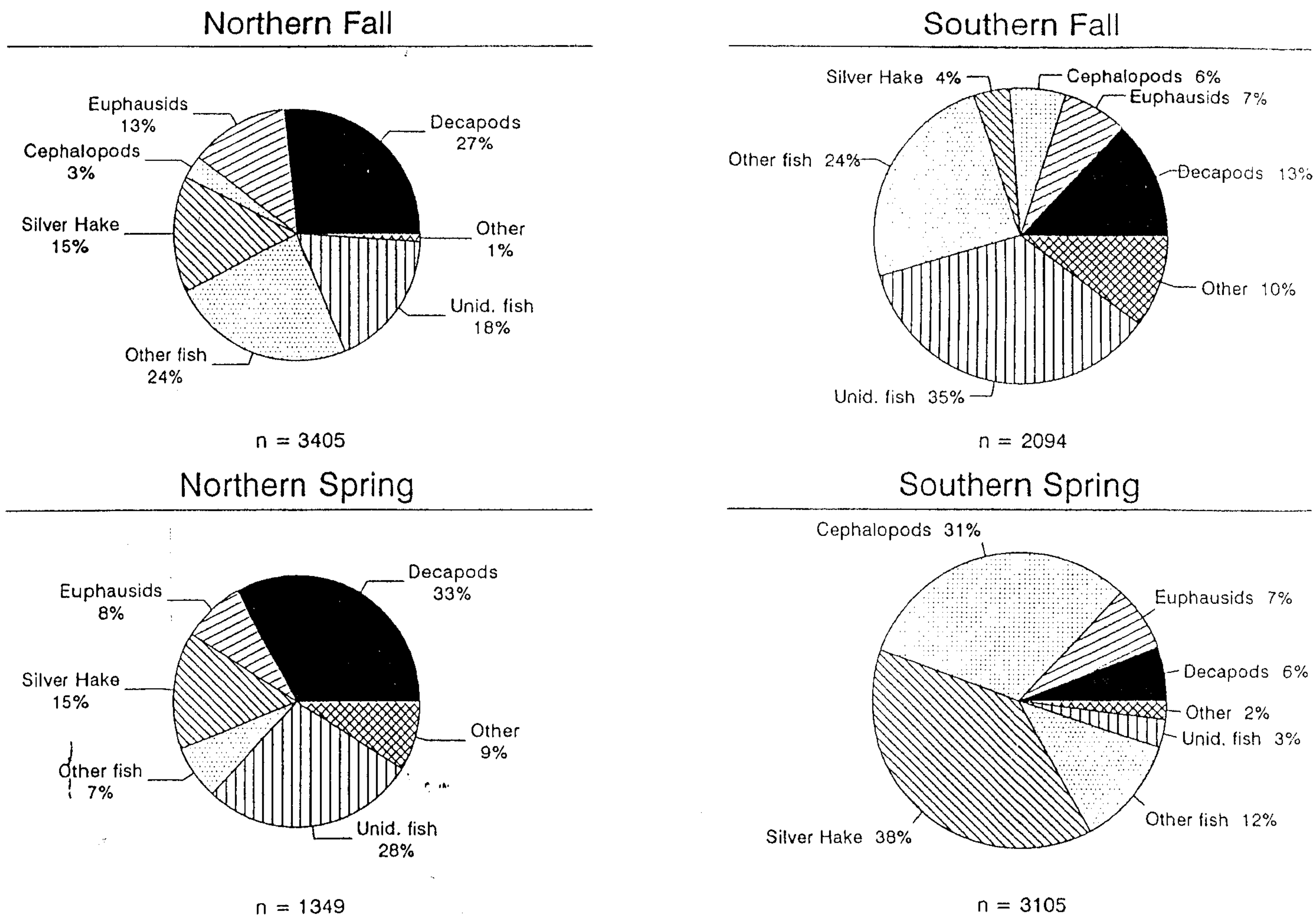

Figure 1. Comparison of the major diet components of 40 cm size class silver hake between northern and southern population groups in spring and autumn. Percentages refer to percent contribution to volume for 1981-90.

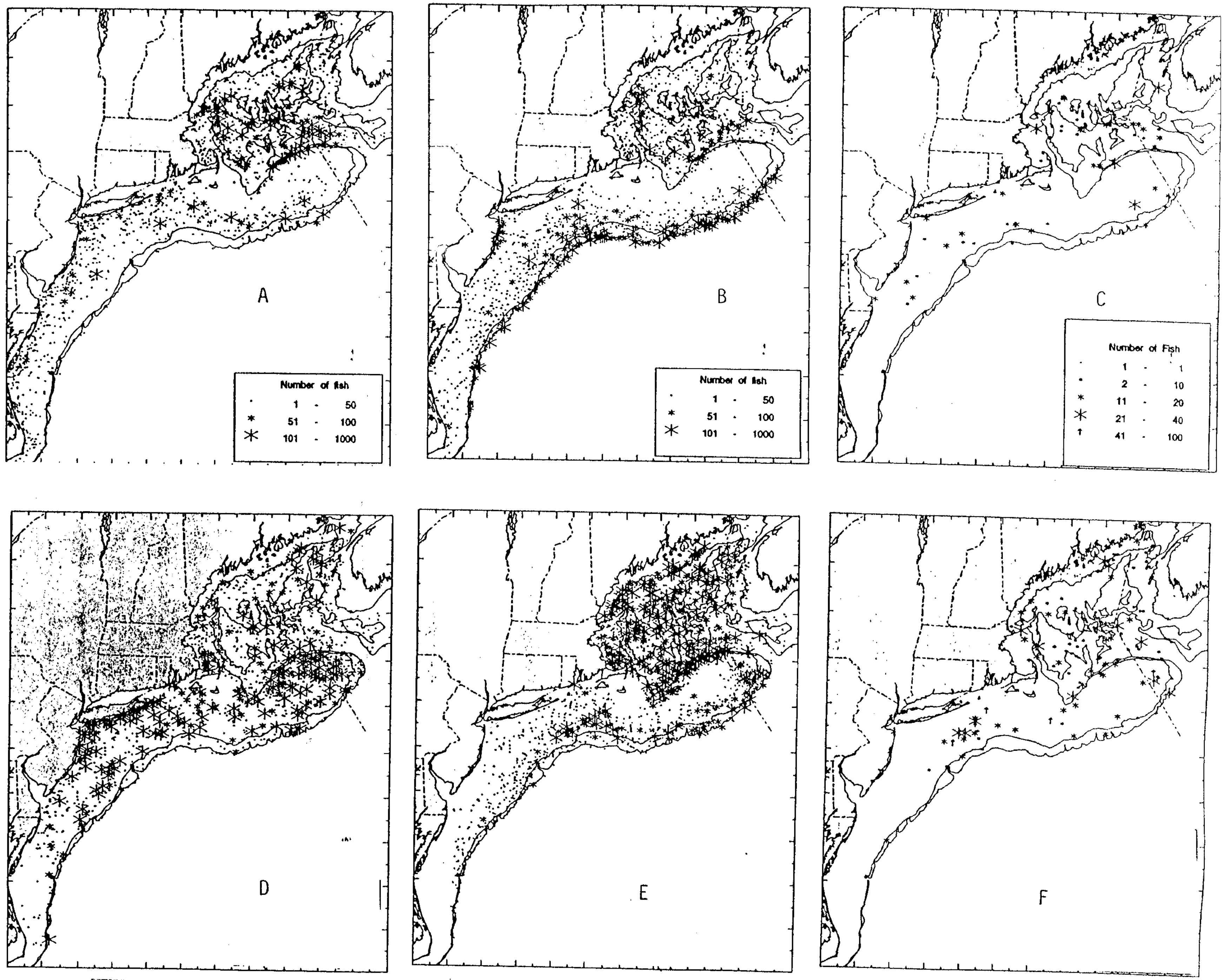

Figure 2. Spring distribution of small (< 20 cm Fl) (A), larger (> 20 cm FL) (B) and percentage cannibalism (C) and autumn distribution of small (< 20 cm Fl) (D), larger (>

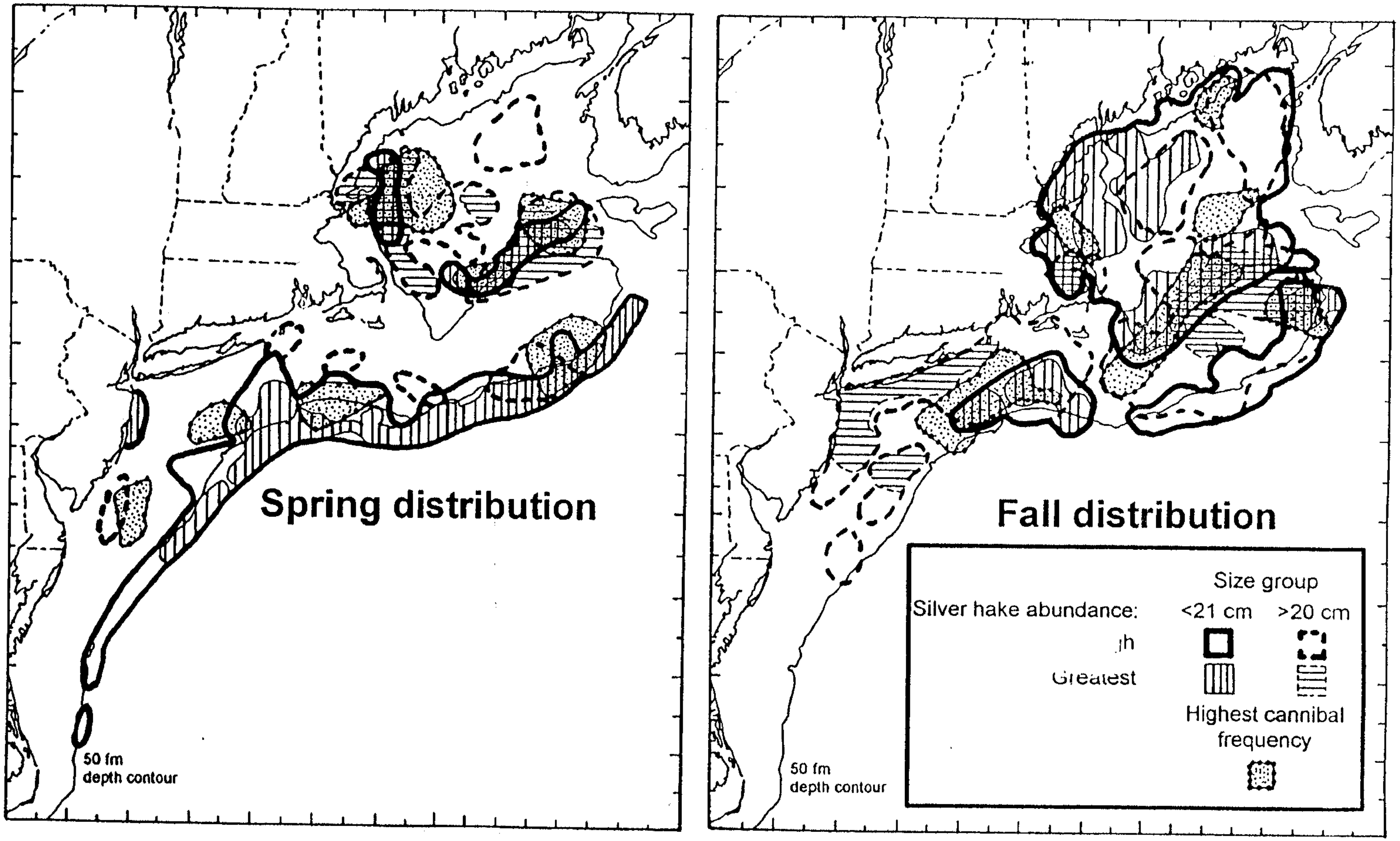

Figure 3. Comparison of the major distribution centers of juvenile and adult silver hake abundance with areas of greatest frequencies of cannibalism for spring and fall during 1981-90.

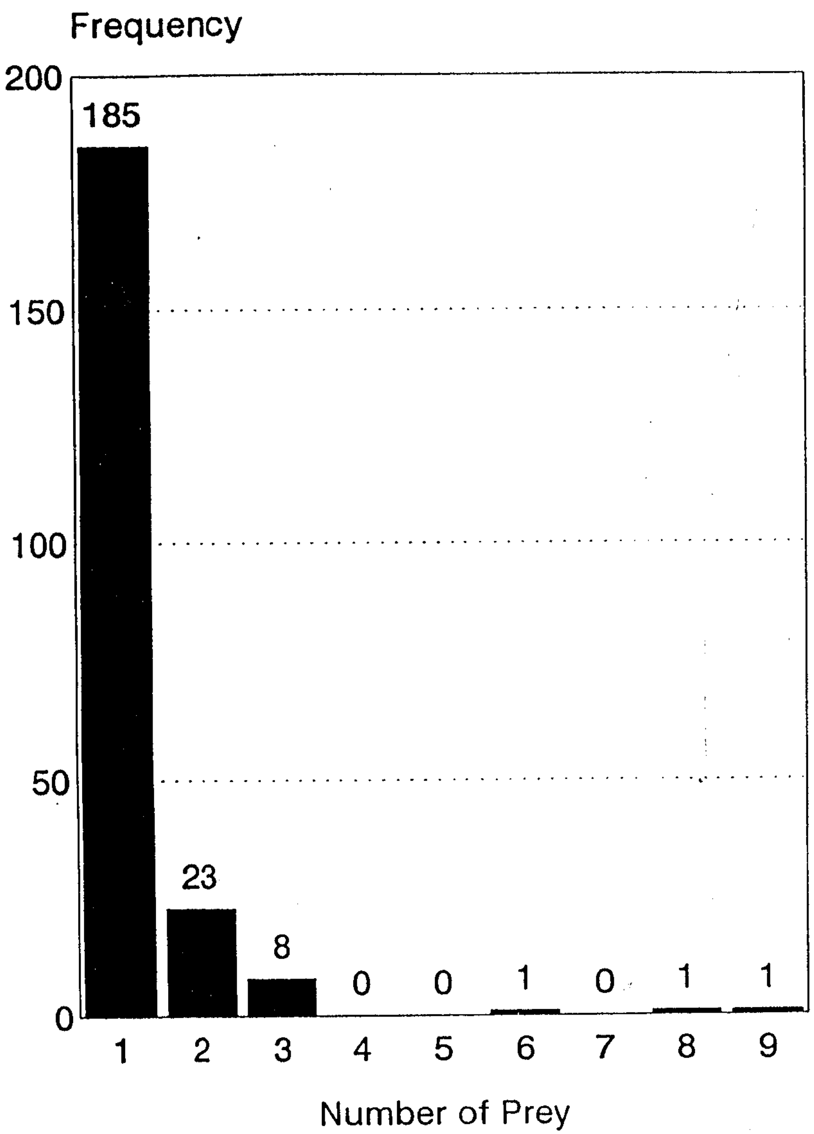

Figure 4. Frequency of occurence of number of silver hake prey in individual conspecifics.

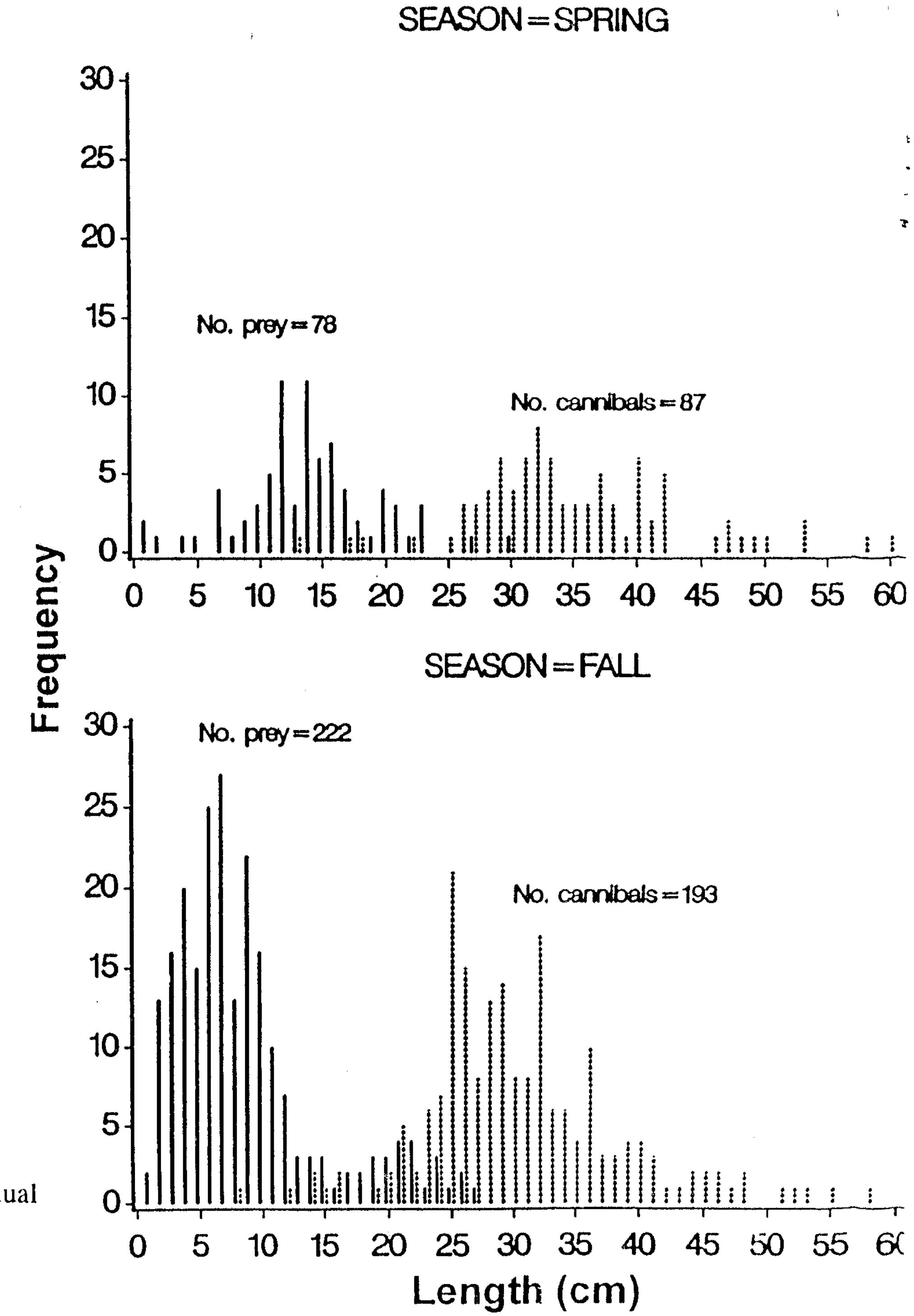

Figure 5. Comparison of silver hake predator and prey lengths

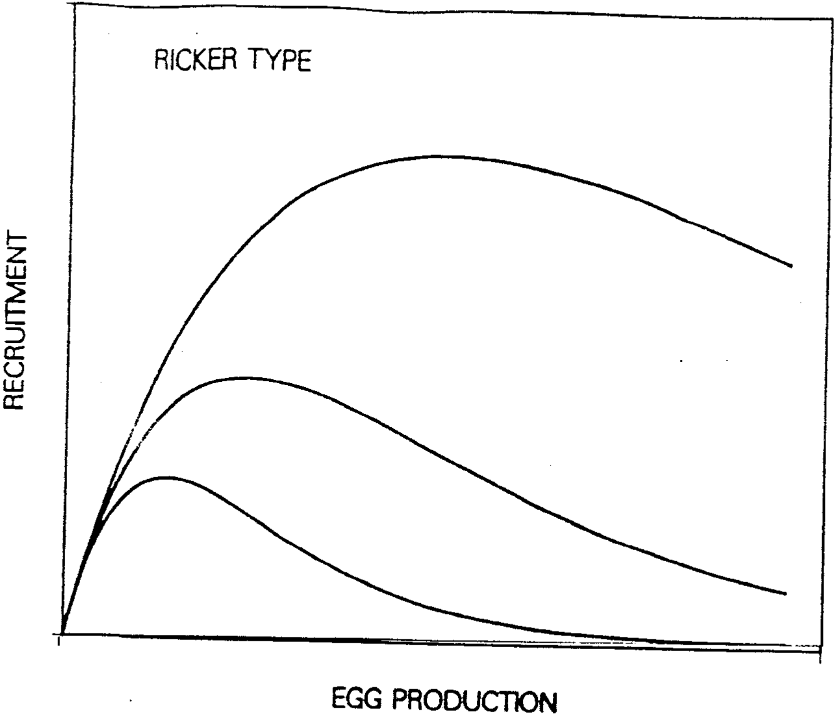

Figure 6. Generalized Ricker model for several levels of the shape parameter.