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GROWTH OF JUVENILE SPINY DOGFISH (<u>SQUALUS ACANTHIAS</u>)
IN THE NW ATLANTIC, WITH PARTICULAR REFERENCE TO THE
EFFECT OF DENSITY-DEPENDENCE

by

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ABSTRACT

MULTIFAN is used to assess possible changes in the growth
of juvenile spiny dogfish sampled during spring cruise surveys
in the Northwest Atlantic. Four-year period runs starting at
1968-1971 are made. Growth is shown not to vary significantly
between sexes during the juvenile stage (i.e., up to age ten),
and pooled length frequency data sets are consequently used in
the analyses. The growth rate is shown to increase from the
first period (1968-1971) to the third period (1976-1979) and
then decrease to the last period considered (1988-1990). The
hypothesis that these changes were density-dependent is tested.
Except for age two, mean lengths at ages one through five are
significantly correlated with mean number of juveniles per tow.

INTRODUCTION

Elasmobranchs lack the calcified structures commonly used
for aging teleosts, such as scales and ototiths. Even when
dorsal spines are present, as in the spiny dogfish, or vertebral
centra are well calcified for aging purposes, traditional and
contemporary methods of validation are often not applicable.
Thus, age and growth studies have been done for several species
of elasmobranchs utilizing length frequency analysis, captivity
records, tag returns, tooth replacement rates, tetracycline
injection, and back calculation and growth model parameters
(Hoenig, 1979; Cailliet et al., 1983; Cailliet et al., 1986,
and; Cailliet, 1990).
   Analyses of spiny dogfish age and growth have been
presented worldwide (Kaganovskaia, 1933 for the Northwest
Pacific; Bonham et al., 1949, Ketchen, 1975, and McFarlane and
Beamish, 1985 for the Northeast Pacific; Aasen, 1963; Holden and
Meadows, 1962, and Fahy, 1989 for the Northeast Atlantic, and;
Templeman, 1944, Soldat, 1982, Slauson, 1982, and Nammack, 1982
for the Northwest Atlantic). These authors aged fish by counting
annuli in dorsal spines, except for Templeman (1944) who
calculated the growth rate of mature females from differences in
length between females at known stages of pregnancy. Also,the
problems of validation of age determination from spines are
discussed by these and other authors (e.g. Jones and Geen,

1977a; Beamish and McFarlane, 1985, and; Tucker, 1985).

Beamish and McFarlane (1985), interpreting annuli from spiny dogfish that were injected with oxytetracycline and recaptured, demonstrated that some previous studies have underestimated the age of the species, resulting in a misunderstanding of important life history parameters.

Fahy (1989) calculated the growth parameters of spiny dogfish in the Southwest Ireland. Results of this work compared well with those obtained by Holden and Meadows (1962).

Elasmobranchs in general, and spiny dogfish in particular, are long-lived animals. This fact makes the use of length-based methods in the estimation of growth parameters inappropriate; due to the expected overlap of the modal lengths of larger, older, individuals. Nevertheless, the method has been used in the past for age verification or validation on spiny dogfish (Bonham et al., 1949; Ketchen, 1975, and; Jones and Geen, 1977b) and on many other elasmobranch species (Olsen, 1954 on the blue shark; Pratt and Casey, 1983 on the shortfin mako; Brander and Palmer, 1985 on skates; Silva, 1988 on the kitefin shark; Skomal, 1990 on the blue shark). Again, Cailliet (1990) gives an extensive literature review of this topic.

The objectives of this study are three-fold: (1) to explore the possibility of utilizing length frequency data in the analysis of growth of the Northwest Atlantic population of spiny dogfish; (2) to use length-based methods to check the validity of the growth studies done by Slauson (1982), Soldat (1982) and Nammack (1982) in the area, and; (3) consistently use the same method to examine possible variations in the growth rate of juveniles in this population.

MATERIAL AND METHODS

Length frequency data were collected from 1968 to 1990 by the National Marine Fisheries Service (NMFS), Woods Hole, Massachusetts, during the spring offshore bottom trawl surveys. These surveys, conducted annually, from Nova Scotia to Cape Hatteras, are based on a stratified random sampling design (NEFC, 1988). Stratified mean number per tow at each centimeter length group, for sexes combined, were extracted from the NEFC/WHOI (Northeast Fisheries Center/Woods Hole Oceanographic Institution) VAX computers using SURVAN (Groundfish Survey Analysis Program).

This information is also available for sexes separated since 1982 but; in order to keep the analysis consistent through the whole period starting in 1968, only data for sexes combined were used. A plot of the frequency data for all one centimeter length-groups is shown in Figure 1. In this plot, a number of modes of varying contrast are apparent up to about 60 centimeters. After, two larger modes can be distinguished. The first one is centered at 75 to 85 centimeters and represents the male and immature female component of the population; while the other one is centered at 85 to 95 centimeters and represents the female component. This study is focused upon the juvenile component of the population, requiring the extraction of only those juveniles from the length frequency data. In order to do that, length frequency for each year was broken through the minimum between 55 and 65 centimeters, and all fish larger than
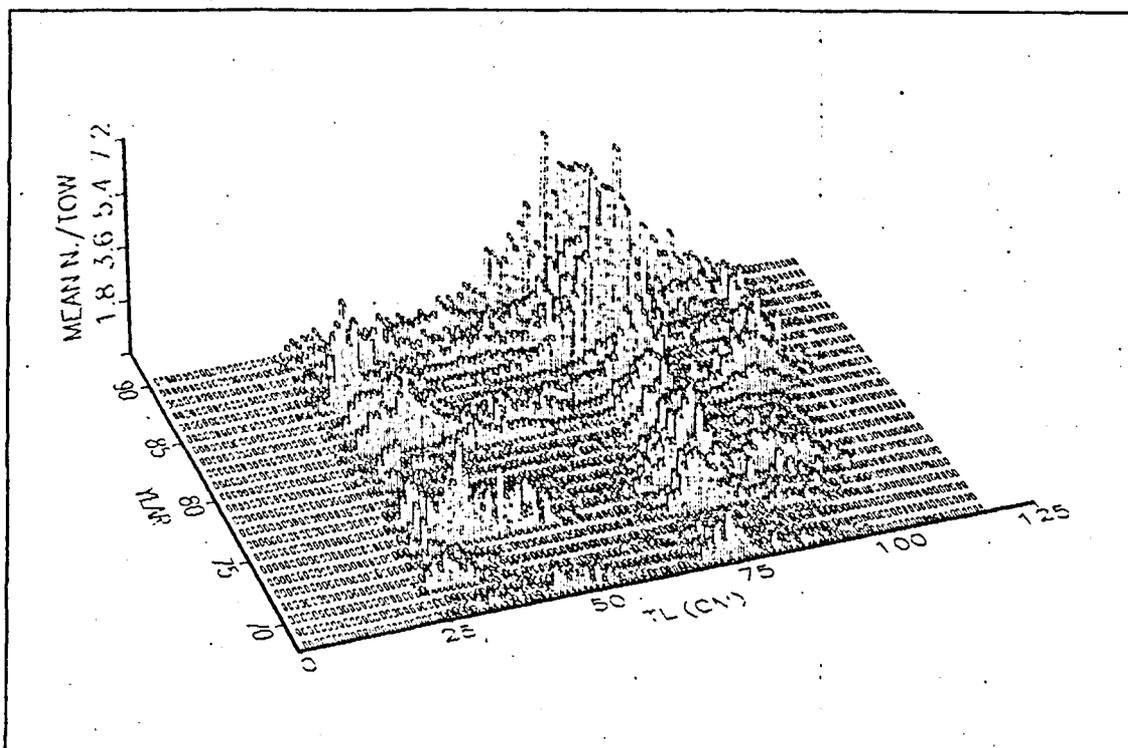
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Figure 1. Spiny dogfish stratified mean number per tow at each centimeter length-group for the period 1968-1990. Data are from sexes combined.

the minima were excluded from the analysis.

MULTIFAN (Fournier et al., 1990) was the method used in the estimation of the growth parameters and age composition of the juvenile spiny dogfish. MULTIFAN is a robust likelihood-based method which simultaneously analyzes multiple length frequency data sets. This method performs hypothesis tests to compare between different models for fitting the data. This way the number of significant age classes which are present in the length frequencies are estimated.

MULTIFAN has several advantages compared to other length frequency methods such as SRLCA (Sheperd, 1987) and ELEFAN I (Pauly and David, 1981). SRLCA has been shown to perform better than ELEFAN I (Basson et al. 1988). Terceiro et al. (1990) have compared the performance of MULTIFAN and SRLCA by applying the two methods to Gulf of Main northern shrimp length frequency samples and concluded that MULTIFAN offered a much more complex but powerful estimation technique, consistently performing better than SRLCA in matching the true patterns of recruitment, proportion at age, and mean length at age.

The log-likelihood function employed in MULTIFAN is (Fournier et al., 1990):

$$\mathcal{L} = -\frac{1}{2} \sum_{\alpha=0}^{N_A} \sum_{i=1}^{N_I} \ln[2\pi(\xi_{i\alpha} + \frac{.1}{N_I})] - \sum_{\alpha=1}^{N_A} N_I \ln(\tau_\alpha)$$
$$+ \sum_{\alpha=1}^{N_A} \sum_{i=1}^{N_I} \ln\{\exp[-\frac{(\tilde{Q}_{i\alpha} - Q_{i\alpha})^2}{2(\xi_{i\alpha} + .1/N_I)\tau_\alpha^2}] + .01\}$$

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If relative abundance data is included in the estimation procedure the quantity:

$$p \sum_{i=1}^{N_A} [\ln(A_i) - \ln(\sum_{j=1}^{N_j} R_{ji})]^2$$

is subtracted from the log-likelihood function;
Where:
i   Subscript indexing the length frequency intervals.
j   Subscript indexing the age classes.
a   Subscript indexing the length frequency data sets.
A_i Value of a relative abundance index in year i.
N_j Number of age classes present in the data sets.
N_A Number of length frequency data sets.
N_i Number of length intervals in each length frequency data set.
p   Penalty weight term reflecting how well the predicted relative abundance fits the true relative abundance.
R_{ji} One of the possible number of age classes j in year i (N_{ji}).
Q_{ia} Probability that a fish picked at random from the fish which composed the ath length frequency data set has a length lying in length interval i.
$\tilde{Q}_{ia}$ Proportion of fish in the ath length frequency data set having a length lying in length interval i.
τ_a Parameters determining the overall variance of the sampling errors in the ath length frequency data set.
ξ_{ia} Parameters determining the relative variances of the sampling errors within the ath length frequency data set.

In order to run MULTIFAN some compromise had to be made between the necessary confidence in the results, which increases with increased number of annual samples in each analysis (up to five in the version of MULTIFAN used); and the resolution of the results in terms of possible changing trends in the growth rates for each period. Further, in order to optimize the analysis of density-dependent growth; the periods should correspond to periods of high and low abundance. After some initial runs a choice of four-year runs was made, starting with the period 1968-1971 and ending with the period 1988-1990, for a total of six analyses. Also, the comparison of the results from the analyses required that the methods and the options within MULTIFAN be consistent. The following choices were made for each four-year analysis: (1) only the first mode in each year was selected to initialize the search in the model setup; (2) four initial guesses of the von Bertalanffy K were made (0.025, 0.050, 0.075, and 0.100), and; (3) seven guesses were made about the number of age classes in the length frequency samples. Two other searches were then made: a systematic active search of the standard deviations around the mean lengths at age; and a search allowing von Bertalanffy K to vary out of the initial parameter space. The latter allowed an active search for the best estimate of K. Also, the runs were made by invoking the survey sample parameterization.
    Pooling length frequency data for the two sexes requires that no differences exist between the mean lengths at age within

the length-groups considered. Mean lengths at age as estimated by different authors suggest that no differences exist between the two sexes in the area (Soldat, 1982; Nammack, 1982), and elsewhere (e.g. Holden and Meadows, 1962, and Fahy, 1988 in the Northeast Atlantic; Ketchen, 1975 in the Northeast Pacific). However, this was never statistically inspected. In order to check the validity of the method proposed in this study, least squares nonlinear regression of the observed lengths on the estimated ages from Nammack were performed for each sex. The von Bertalanffy growth equation:

$$L_t = L_\infty \{1 - \exp[-K(t - t_0)]\}$$

was used;
Where:
t   Age in years.
L_t Length of the fish (in cm) at age t.
L_∞ Asymptotic length.
K   Brody growth coefficient.
t_0 Theoretical age at zero length.

    Then, the null-hypothesis that the male and female samples, for each age-group, came from populations having the same mean was tested. Non-parametric, Mann-Whitney's tests were performed (Sokal and Rohlf, 1981).
    Recomputation of Nammack's (Nammack, 1982) and Soldat's (Soldat, 1982) spiny dogfish von Bertalanffy growth parameters were done by regressing the annual increments at length against initial length, from (Gulland, 1983):

$$L_{t+T} - L_t = (L_\infty - L_t)[1 - \exp(-KT)]$$

Where T is the length of the time interval (set to one in this case), and all the other symbols are as in the equation above.
    Then, t_0 was estimated from:

$$t_0 = t + \frac{1}{K} \ln \frac{L_\infty - L_t}{L_\infty}$$

    The estimated parameters were then used as inputs for a least squares nonlinear regression reestimation.
    Only lengths at juvenile ages (i.e., ages zero through six) were used in the parameter estimations, L_∞ and K being allowed to take any values out of the biologically reasonable boundaries. This technique was used in order to make the results comparable. The actual observations were used to recompute Nammack's (1982) growth parameters estimation and observed mean lengths at age to Soldat's (1982). This author's samples were collected from the southern Scotian Shelf to Cape Hatteras during a cooperative USA-USSR bottom trawl survey in February-March 1978. Nammack's samples were collected in the Southern New England area, during April-May 1980 (over 90%) and 1981, from the NEFC spring offshore bottom trawl surveys. Though Nammack used also samples collected elsewhere, in other periods of the year, only the age estimates from the samples referred above were included in the recomputation.
    In order to correct for the two months time delay between the periods when Nammack's (1982) and Soldat's (1982) samples

were collected all spiny dogfish ages t from Soldat were reassigned as ages t - 0.167. Further, all ages estimated by Soldat were reduced by one year due to the apparent misinterpretation of the time of birth.

The growth curves estimated by Slauson (1982) were not used in the analysis for two reasons. Firstly, no information on the mean lengths at age is given, which prohibits the recomputation of the growth parameters. Secondly, the samples were collected during a large period of time (i.e., from 1976 to 1981), but no information is presented about the relative sample sizes which does not allow an estimate of the mean sampling time.

In order to compare the growth curves from Nammack (1982) and Soldat (1982) with the MULTIFAN estimates, and given the different time scales considered in each analysis (i.e., the time lag between the samples from Nammack and Soldat is two years and does not coincide with the years included in any of the analysis performed in this study), another run was done using MULTIFAN with length frequency samples from 1978 to 1980. The same setup choices were made in this run, except for the parameterization as unstructured samples instead of survey samples.

Density-dependence was analyzed by performing correlation analyses between mean number of juveniles (for the same sizes included in the analyses of growth) in each period and the respective mean lengths at age. A non-parametric correlation test, Kendall's rank correlation, was used (Sokal and Rohlf, 1981).

RESULTS

Validation of the Method

Results of the analysis of spiny dogfish growth using the estimated lengths at age from Nammack are summarized in Table 1 and Figure 2. Males and females have distinct growth parameters with the females reaching larger sizes, as indicated by the larger L_∞, which they approach at lower rates of growth (K). Nevertheless, the mean lengths of both sexes up to at least age ten are very similar. Results from the application of Mann-

Table 1. Von Bertalanffy growth parameters from estimated lengths at age by Nammack.

	L_∞	K	t_0	N	r^2
Males	81.32	0.1578	-2.4523	479	0.9598
Females	100.34	0.1128	-2.5520	958	0.9614

Whitney's tests of the null-hypothesis (H_0) that the male and female samples come from populations having the same mean are presented in Table 2. H_0 is rejected if the test statistic is too large. As expected, H_0 was not rejected up to age ten (P > 0.05), strongly suggesting that the growth of juveniles can be pooled. The larger sizes of the females is reflected by the negative values of the test statistics after age 9.
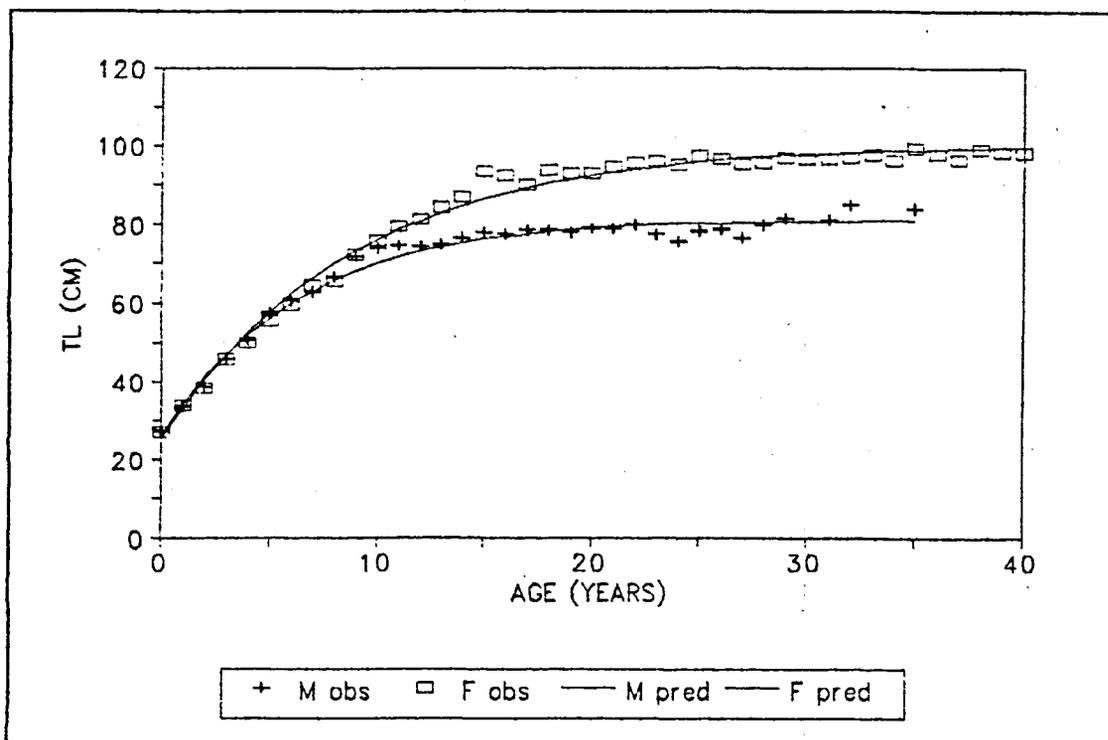
Figure 2. Mean observed lengths at age (obs) and fitted von Bertalanffy growth curves (pred) from samples collected on spring 1980 and 1981. Males (M) and females (F) shown (data from Nammack).

Table 2. Results of Mann-Whitney's tests of differences between the mean lengths at age (L_i). Average ranks (AR) and numbers (N) for males (M) and females (F) are shown. Test statistics (Z) and probabilities (P) are also shown.

	AR_M	AR_F	N_M	N_F	Z	P
L_0	77.839	77.093	84	70	0.1035	0.9176
L_1	37.597	42.012	36	43	-0.8599	0.3898
L_2	40.427	37.375	41	36	0.5964	0.5509
L_3	27.531	27.455	32	22	0.0089	0.9929
L_4	35.109	31.985	32	34	0.6561	0.5117
L_5	29.227	22.571	22	28	1.5997	0.1097
L_6	23.292	22.667	24	21	0.1485	0.8819
L_7	14.875	15.917	12	18	-0.2972	0.7663
L_8	15.763	15.046	19	11	0.1944	0.8458
L_9	11.818	13.929	11	14	-0.6880	0.4914
L_{10}	7.000	10.214	4	14	-1.0126	0.3113
L_{11}	6.667	11.539	6	13	-1.7255	0.0844
L_{12}	3.200	12.429	5	14	-3.1152	0.0018
L_{13+}					< -2	< 0.01

MULTIFAN Analyses

Results of X^2 tests on the increments of the twice the log-likelihood functions from the models picked as best candidates are presented in Table 3. All the increments are accepted at the 0.9 probability level. At the 0.95 probability level the fit

Table 3. Results of X^2 tests (α values) on the increments of the twice the log-likelihood function values (L) chosen as best candidates in each four year period since 1968.

	68-71	72-75	76-79	80-83	84-87	88-90
L	2972.87	2909.38	2930.76	2912.86	3112.41	2183.92
α	< 0.001	0.024	< 0.001	0.077	< 0.001	0.002
df	1	1	1	1	4	1

corresponding to the 1980-1983 period is, however, rejected. Similarly, active searches of K beyond the initial parameter space led to the estimates of the von Bertalanffy K and L∞ growth parameters given in Table 4. Since only juveniles were selected for this study, and von Bertalanffy growth curves were fit through the length frequency modes, the values of L∞ and K are meaningless in absolute terms.

Table 4. Von Bertalanffy growth parameters K and $L_{\bullet}$ in each four- year period considered in the analises. Mean lengths at age (L_i) and the respective standard deviations (SD_i) are also presented.

	68-71	72-75	76-79	80-83	84-87	88-90
L_∞	274.6	161.8	367.3	72.1	92.5	100.1
K	0.023	0.048	0.019	0.196	0.105	0.077
t_0	-4.85	-4.01	-4.25	-3.21	-3.51	-4.24
L_0	29.28	28.45	28.67		28.46	27.84
SD_0	2.41	1.98	1.91		2.32	2.30
L_1	34.91	34.74	35.10	33.72	34.83	33.18
SD_1	2.35	2.14	2.03	5.03	2.06	2.34
L_2	40.42	40.73	41.40	40.56	40.56	38.13
SD_2	2.29	2.30	2.15	4.38	1.84	2.39
L_3	45.79	46.44	47.58	46.17	45.72	42.71
SD_3	2.23	2.46	2.28	3.91	1.67	2.43
L_4	51.04	51.88	53.63	50.78	50.37	46.95
SD_4	2.18	2.62	2.41	3.56	1.53	2.46
L_5	56.18	57.06	59.59	54.58	54.56	50.88
SD_5	2.13	2.79	2.55	3.30	1.41	2.50
L_6	61.19			57.69	58.33	54.52
SD_6	2.08			3.10	1.31	2.53
L_7						57.89
SD_7						2.56

It is apparent, from Table 4, that the number of age groups increased in the three last periods considered in the analyses, consequently decreasing the mean lengths at age. In 1980-1983 ages zero and one show a larger overlap, mostly in 1981 and 1983. This resulted in the mode corresponding to age one being the first mode detected, and its mean length probably slightly underestimated, which justifies the rejection of this fit at the 0.95 probability level.

Figure 3 presents the von Bertalanffy growth curves as estimated in the present study. A slight increase in the
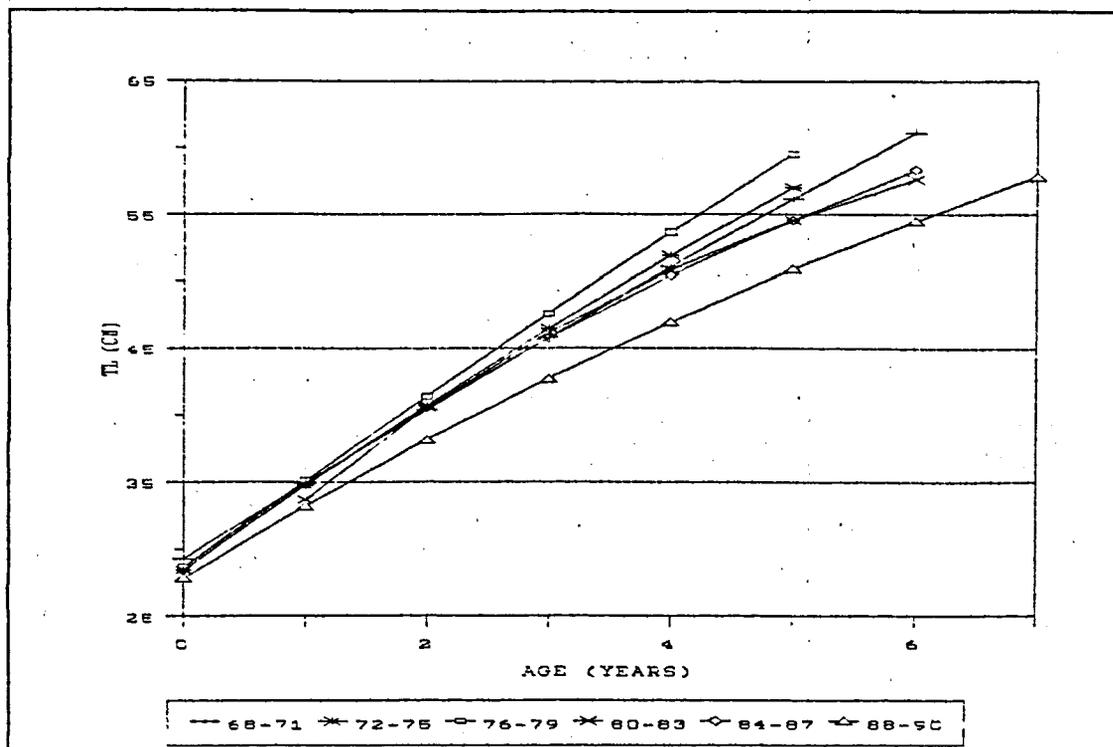
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Figure 3. Mean lengths at age for different periods, predicted by fitting von Bertalanffy growth curves using MULTIFAN.

relative growth rate is apparent from the first period (1968-1971) to the second period (1972-1975). Then, the relative growth rate increases even further to the third period. During the two periods analyzed from 1980 to 1987 the relative growth rates exhibit some stationarity. Finally, in the last period considered the growth rate shows a considerable decrease.

Growth Comparisons

In order to compare the performance of MULTIFAN with the performance of aging by direct methods, namely with the results from Nammack (1982) and Soldat (1982), a run was done using MULTIFAN with length frequency data from 1978 to 1980.

The comparative results of the recomputed growth parameters and observed mean lengths at age from the two aforementioned authors are presented in Table 5 and Figure 4. The parameter values and mean lengths at age, as predicted by MULTIFAN, are also presented. Though the growth curve recomputed from Soldat (1982) clearly approaches a lower asymptote and exhibits a

Table 5. Comparative von Bertalanffy growth parameters and mean lengths at age as predicted from MULTIFAN, with data from 1978-1980, and from Nammack's (1982) and Soldat's (1982) data after recomputation.

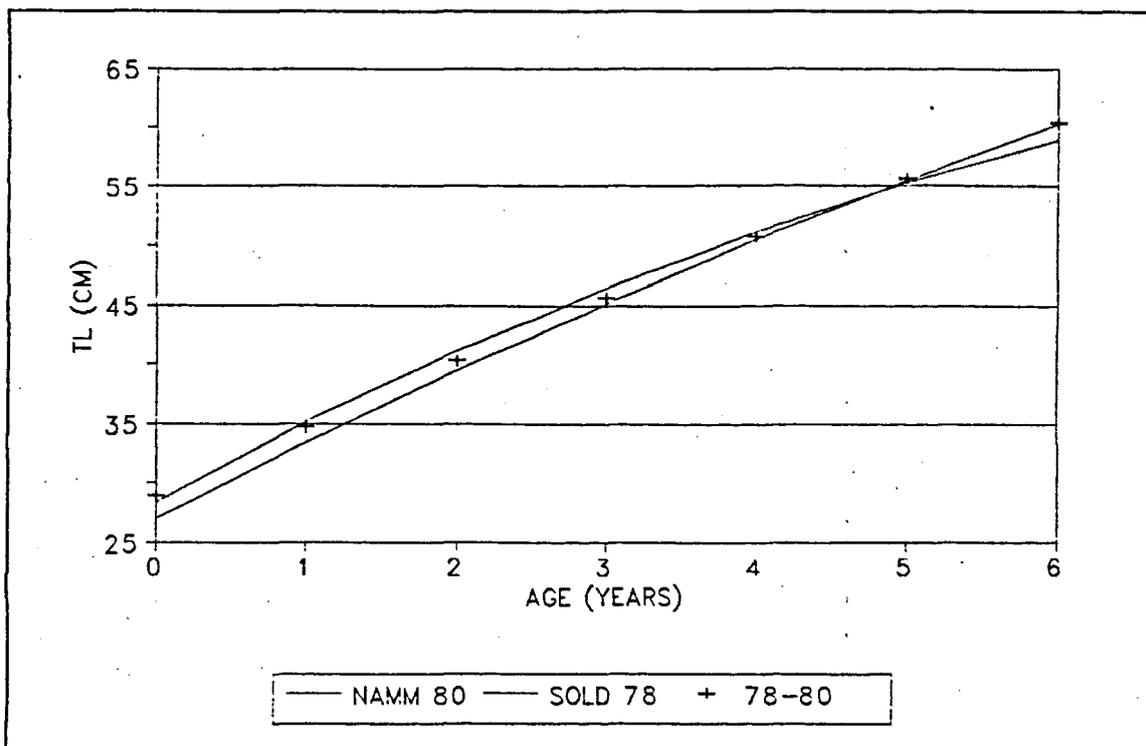|	L_∞	K	t_0	L_0	L_1	L_2	L_3	L_4	L_5	L_6
NAMMACK	132.7	0.063	-3.61	27.0	33.5	39.5	45.2	50.5	55.5	60.3
SOLDAT	86.3	0.125	-3.19	28.3	35.1	41.1	46.4	51.1	55.2	58.9
78-80	172.5	0.041	-4.46	28.9	34.7	40.3	45.6	50.7	55.6	60.4

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Figure 4. Mean lengths at age predicted by fitting von Bertalanffy growth curves to Nammack's (1982) (data from 1980 and 1981) and Soldat's (1982) (data from 1978) spiny dogfish juvenile mean lengths. The predicted mean lengths at age as estimated from this study in the period 1978 to 1980 is also shown.

larger growth rate than the growth curve recomputed from Nammack's data, the differences between the predicted mean lengths of juveniles are clearly very small (in the order of 1.5 cm for ages zero through two, and age six). Further, the predicted mean lengths from MULTIFAN compare very well with both growth curves.

Analyses of Density-Dependence

Given the apparent changes in the growth rates of the juveniles since 1968, the hypothesis that these changes may be density-dependent should be analyzed. Given the segregative behavior of this species, with adult males and females as well as juveniles making their one schools, the indices of abundance against which the mean lengths at age should be analyzed for testing the validity of this hypothesis are the abundance of juveniles. A plot of the mean lengths at ages one through five in each of the six periods considered, as well as the respective mean numbers per tow, are shown in Figure 5. It is apparent from the analysis of this figure that: (1) there is a negative correlation between the mean lengths at each age and the indices of abundance, and; (2) the density-dependence signal is amplified for larger ages. (1) suggests the existence of density-dependence, and (2) results from the cumulative effect of density-dependence throughout the different "cohorts" considered.

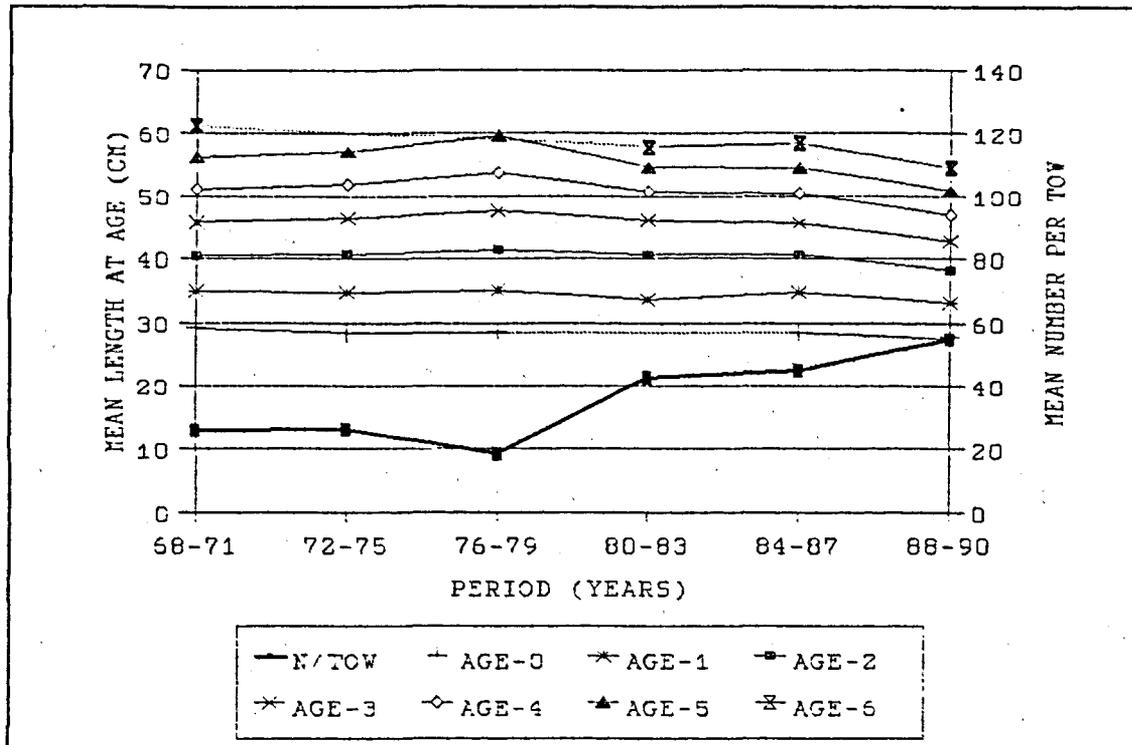Results from a Kendall's rank correlation analysis are

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Figure 5. Mean lengths at age as estimated from MULTIFAN and mean number of juveniles per tow in each four year period starting in 1968 to 1971.

given in Table 6. Both the correlation coefficients and the significance levels at which these coefficients are accepted, for samples of size six, are shown in the correlation matrix.

Mean lengths at age two are not significantly correlated with mean number per tow ($\tau = -0.552$; $\alpha > 0.1$). Significant negative correlations are found for ages one and three ($\tau = -0.733$; $\alpha < 0.05$), and ages four and five ($\tau = -0.867$; $\alpha \ll 0.05$).

Table 6. Kendall's rank correlation matrix of mean number of juveniles per tow ($\bar{N}$) and predicted mean lengths at age ($\bar{L}_i$). The rank correlation coefficients and (significance levels), for samples of size six, are presented.

	$\bar{N}$	$\bar{L}_1$	$\bar{L}_2$	$\bar{L}_3$	$\bar{L}_4$	$\bar{L}_5$
$\bar{N}$	1.000	-.733	-.552	-.733	-.867	-.867
	(1.000)	(.039)	(.126)	(.039)	(.015)	(.015)
$\bar{L}_1$	-.733	1.000	.414	.467	.600	.600
	(.039)	(1.000)	(.251)	(.189)	(.091)	(.091)
$\bar{L}_2$	-.552	.414	1.000	.828	.690	.690
	(.126)	(.251)	(1.000)	(.022)	(.056)	(.056)
$\bar{L}_3$	-.733	.467	.828	1.000	.867	.867
	(.039)	(.189)	(.022)	(1.000)	(.015)	(.015)
$\bar{L}_4$	-.867	.600	.690	.867	1.000	1.000
	(.015)	(.091)	(.056)	(.015)	(1.000)	(.005)
$\bar{L}_5$	-.867	.600	.690	.867	1.000	1.000
	(.015)	(.091)	(.056)	(.015)	(.005)	(1.000)

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DISCUSSION

    This technique of extracting only juvenile lengths from the
whole length frequency data sets for growth analysis using
MULTIFAN, while not allowing for the estimation of growth for
the whole life-span of a population, is an alternative to aging
elasmobranchs from hard structures (i.e., spines and vertebrae)
when the growth bands are unclear in those structures. Even when
spines and/or vertebrae can be used for aging purposes, as in
the present case, this technique can either be used as a
validation method or in the assessment of changes in growth over
a large period of time. Alternative methods for the analysis of
length frequencies (e.g. ELEFAN and SRLCA) are less robust if
this technique is to be used, given that L_{∞} becomes an input
parameter and the lack of length frequencies between the larger
length used and the values guessed for L_{∞} decreases precision
(Silva, unpublished analyses). On the other hand, if the whole
length frequency is to be used, the analyses become too noisy
and the models will tend to maxima out of realistic parameter
space.

    The comparison of the estimated ages from the growth
analyses using MULTIFAN with those estimated from Nammack (1982)
indicates that only some juvenile ages (up to eight ages in
1988-1990) were included in the analyses. This suggests that
juvenile lengths at ages greater than seven overlap with the
adult male and pre-adult female modes, i.e., the first large
mode in the length frequencies (Figure 1).

    There seems to be no apparent reason why age two should not
grow density-dependently when ages one and three do exhibit
density-dependent growth. These results do however suggest,
together with the analysis of Figure 5, that density-dependence
increases towards larger ages. This would mean that though most
of the prey items are shared between all juvenile age groups,
the younger spiny dogfish will also have an intra-cohort
competition which decreases in favor of a stronger intra-life-
stage competition as they approach age four.

    Nammack (1982) performed a cluster analysis of size (in 5
cm length-groups) by diet. As a result of this analysis six
separate feeding size-classes of dogfish were detected: 21-30
cm; 31-35 cm; 36-55 cm; 56-65 cm; 66-100 cm; and 101-110 cm.
These classes can be assigned to respectively ages: 0; 1; 2-3-4-
5; 6-7-8; and >8 for the two larger size-classes (Figure 2).
Interestingly, the higher index of similarity among the 36-55 cm
feeding size-class is between the 36-40 cm (age-2) and the 46-50
cm (age-4) length-groups. The similarity than decreases for the
41-45 cm (age-3) length-group and it decreases even further for
the 51-55 cm (age-5) length-group.

    This indicates that the results from an analysis of
density-dependence can be strongly influenced by the feeding
behavior of the population under study, in particular by the
possible segregation into different life-stages which will tend
to feed on distinct prey items (See Nikolskii, 1969, and
Weatherley and Gill, 1987 on this subject). Thus, the different
carrying capacities of each life-stage will require that an
individual analysis be performed for each group.

    This is a first study showing the existence of density-
dependent growth in an elasmobranch population. Though several
studies have showed growth not to be density-dependent in some

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fish populations (e.g., Hempel, 1955 in the North Sea adult plaice; LeCren, 1958 in perch in Windermere; Gulland, 1970, and Jones and Hislop, 1978 in the North Sea haddock, and; Holden, 1978 in other fish species in the North Sea), many other studies have demonstrated that growth varies in a density-dependent way (El-Zarka, 1959 and, Eshenroder, 1977 in yellow perch in Saginaw Bay; Wells, 1977 in yellow perch in Lake Michigan; Iles, 1968 in North Sea herring; Pitt, 1975 in the Grand Bank American plaice; Peterman, 1984 in early ocean life of sockeye salmon; Valiela, 1984 in herring in the Gulf of St. Lawrence).

The Northwest Atlantic population of spiny dogfish was at high density during the period of this study (Murawski and Almeida, 1990) which may explain the clear correlation between most lengths at ages and indices of abundance. The North Sea populations of plaice and haddock suggestly did not show marked responses in growth to the increase in abundance from the pre- to the postwar periods due to their abundances considerably below the carrying capacity of the North Sea (Gulland, 1970, and Jones and Hislop, 1978). Similarly, Anthony and Fogarty (1985), found growth to be density-dependent, in the Atlantic herring, only during time periods when abundance was high, and the same was observed by Ross and Almeida (1986) for the silver hake in the Gulf of Main. When abundance was low, in both studies, growth became correlated with water temperature. Ross and Nelson (in press), also found higher correlations between growth rates of yellowtail flounder and haddock, on Geoges Bank, during periods of high stock abundance than at times when stocks were depleted.

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