REPRODUCTIVE STRATEGIES OF
SPINY DOGFISH, *SQUALUS ACANTHIAS*, IN THE NW ATLANTIC

by

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ABSTRACT

Fecundity and size at maturity of spiny dogfish in the Northwest Atlantic were investigated. Literature data from samples collected since 1942 was reanalyzed and compared with more recent data collected during the 1980s and 1991. Significant negative correlations were detected between fecundity and the abundance of the smaller size-classes (80-84, 85-89 and 90-94 cm) but not the larger size-classes (95-99 and 100-104 cm). Conversely, positive, mostly nonsignificant correlations, were found between fecundity and the mean weight of a mature female. Changes in the size at 50% female maturity were also detected and were suggested to be the result of density-dependent changes in juvenile growth.

INTRODUCTION

Elasmobranchs are considered K-strategists, which are characterized by slow development, late maturity, small reproductive effort, few young, and long life (Pianka, 1970; Stearns, 1976). However, the flat growth curve exhibited by spiny dogfish in the Northwest Atlantic (Silva, 1992; Silva, 1993a) suggests that their reproductive effort is actually high. Indeed, this is the form of the growth curve for most small pelagic fish species (Ni, 1978). Unlike small pelagic species, spiny dogfish allocate energy to quality (large size) rather than quantity of offspring, consequently increasing the survival rate of the young fish. Thus, mortality, which plays a trade-off with reproduction and growth (Charnov and Schaffer, 1973; Schaffer, 1974a; Schaffer, 1974b; Stearns, 1976; Bell, 1976; Bell, 1980; Stearns and Crandall, 1981; Roff, 1982; Roff, 1984), is reduced in sharks in general and in spiny dogfish in particular. This reduced mortality is evidenced by the high longevity and iteroparity of most shark species (Hoenig and Gruber, 1990; Anderson, 1990).

The spiny dogfish is an ovoviviparous species, or aplacentally viviparous according to some authors who do not recognize ovoviviparity in chondrichthyan fishes (Teshima et al., 1971; Wourms, 1977; Wourms et al., 1988; Otake, 1990).

Reproductive dynamics are better understood for the spiny dogfish than most other sharks. Studies have been done in New Zealand (Hanchet, 1988), the Black Sea (Kirnosova, 1989) and the Northwest Pacific (Kaganovskaia, 1933; Kaganovskaia, 1937; Yamamoto and Kibezaki, 1950; and, Anon. 1956), but the most intensively-studied areas have been in

the Northeast Pacific (Hart, 1942; Bonham et al. 1949; Ketchen, 1972; Ketchen, 1975; Jones and Geen, 1977; Wood et al., 1979; McFarlane et al., 1984), the Northeast Atlantic (Ford, 1921; Hickling, 1930; Holden and Meadows, 1964; Holden, 1974; Gauld, 1979; Fahy, 1988; Fahy, 1989a; Fahy, 1989b; and, Fahy and Gleeson, 1989), and the Northwest Atlantic. Templeman (1944) published one of the most comprehensive studies focusing upon reproduction of the Northwest Atlantic spiny dogfish population. More recent studies have been published by Bigelow and Schroeder (1953), Jensen et al. (1961), Jensen (1966), Soldat (1979), Nammack (1982), Slauson (1982), Waring (1984), and Nammack et al. (1985).

Holden (1974) compared the fecundity of the Scottish-Norwegian stock (5.78 eggs/female) with the fecundity estimates given by Templeman for the Northwest Atlantic stock (4.20 eggs/female), and suggested that the differences could reflect a response by the European stock to decreased abundance caused by fishing. Compensatory increases in the fecundity of the Scottish-Norwegian stock of spiny dogfish were later reported to be 42% (Gauld, 1979).

Fecundity studies of spiny dogfish in British Columbia waters showed much smaller changes with an increase from 6.2 (Ketchen, 1972) to 7.3 embryos per breeding female (Jones and Geen, 1977). When compared with earlier estimates of 7.3 embryos per female from the 1940s (Bonham et al., 1949), these changes are probably of little significance. However, the Northeast Pacific population, contrary to the Scottish-Norwegian stock, was subject to a very high level of exploitation during the 1940s, which was later reduced by at least 90% (Wood et al., 1979).

Changes in fecundity were also detected in the Northwest Atlantic population. Nammack (1982) detected an increase in the average fecundity from 3.69 embryos per female during the 1940s (Templeman, 1944) to 6.56 in 1980-1981. Earlier, Soldat (1979) estimated fecundity at 5.81 embryos per female (data from 1970-1978), which is close to the estimated fecundity of 5.80 in 1961 (Jensen et al., 1961; and, Jensen, 1966).

Another important reproductive parameter with implications for lifetime fecundity is the length (and/or age) at 50% maturity. In the Northeast Pacific, Bonham et al. (1949) estimated the length at 50% female maturity was 92 cm, which is close to the estimate of 93.5 cm reported by Ketchen (1972). The length at 50% maturity of 82 cm reported for females of the Scottish-Norwegian stock by Holden and Meadows (1964) is also similar to the 83 cm reported 15 years later by Gauld (1979). Fifty-percent maturity estimates from Southwest Ireland over a lag of 60 years show a small decrease from 75-80 cm reported by Hickling (1930) to 74 cm reported by Fahy (1989b).

Contrary to the examples above, length at 50% female maturity in the Sea of Japan decreased from 104-107 cm (Anon., 1956) during the 1930s to 90-95 cm (Yamamoto and Kibezaki, 1950; reviewed in Ketchen, 1972). Length at 50% maturity of the spiny dogfish in the Northwest Atlantic was reported as 77 cm in the 1940s (Templeman, 1944), 79 cm in the early- to mid- 1970s (calculated from Soldat, 1979) and 80 cm in 1980-1981 (Nammack, 1982; Nammack, 1985). However small, these results seem to indicate an increasing trend in the size at maturity. Since analyses of juvenile growth indicate density-dependence (Silva, 1992), one should expect that either the length at maturity changed accordingly during the same period or, alternatively, the population displays a fixed-length-at-maturity strategy, in which case age would become the varying parameter.

Changes in the methodologies used in the analyses of either length at 50% maturity or fecundity may mask the existence of compensatory changes in these parameters, the underlying relationships between them, and between these parameters and growth. The objectives of this study are to consistently use the same methods in the analyses of maturity and fecundity from the data in the references above, and more recent

2

data collected in the Northwest Atlantic, to investigate and evaluate possible changes in those parameters.

MATERIAL AND METHODS

Data on the maturity and fecundity of spiny dogfish were collected by the Northeast Fisheries Science Center of the National Marine Fisheries Service (NEFSC/NMFS), Woods Hole, Massachusetts, during offshore bottom trawl surveys conducted in the spring of 1980 and 1981 (Nammack, 1982), autumn 1984, spring 1985, spring and autumn 1986, 1987, and 1988, autumn 1990, and spring 1991. The sampling procedures included separating the catch by sex, weighing the catch for each sex, and sampling the total catch for length. Ten males and ten females were then randomly selected for biological sampling. Each individual fish was again measured for total length to the nearest centimeter, and its reproductive condition was determined.

Males were classified as either immature or mature according to several criteria. When the claspers were undeveloped, the gonads were threadlike, tiny and whitish, and the sperm ducts straight, the fish were classified as immature. A mature male was characterized by the presence of large and stiff claspers, round and reddish gonads filled with flowing sperm, and the sperm ducts tightly coiled. Clasper length measurements were taken in 1980 and 1981 (Nammack, 1982), and again in 1991 (present study). The right claspers were measured and the lengths taken to the nearest millimeter.

Female maturity classification involved the inspection of both ovaries and uteri. Fish with small ovaries, no differentiated eggs, and thread-shaped empty uteri were classified as immature females. When the females either had developed eggs in the ovaries or enlarged uteri (either empty or filled with candles or embryos) they were classified as mature. Fecundity was also analyzed in some years. If large eggs (15-45 mm) of about the same size were present in the ovaries, these were counted. Finally, the number of embryos was also counted and one randomly chosen and measured to the nearest millimeter. In addition to these samples, information collected by Templeman (1944), Jensen (1966), Soldat (1979), and Slauson (1982) is reanalyzed in this study for the purpose of making the results comparable.

Because samples from spring, summer, and autumn were used in the studies above, fecundity estimates from samples collected during NMFS offshore bottom trawl surveys conducted in the autumns of 1984, 1986, 1987, 1988 and 1990, as well as from the springs of 1985, 1986, 1987, 1988 and 1991 were pooled and their means tested for differences using nonparametric Mann-Whitney U-tests (Daniel, 1990). In order to check possible correlations between mean fecundities and mature female abundance indices, as well as between fecundities and mean weights, Kendall's rank correlation analyses were performed (Sokal and Rohlf, 1981).

Male and female maturation ogives were fitted to the proportion mature by 1 centimeter length intervals using a logistic model of the form (Dixon, 1985):

$$P = \frac{\exp(a+bTL)}{1+\exp(a+bTL)}$$

Where P is the proportion mature, TL is the total length in centimeters, and a and b are the intercept and slope parameters. A χ^2 goodness-of-fit test was used to test the hypothesis that the model fits the data adequately. This is computed from the observed versus predicted frequencies at each cell in the data.

In addition, male length at 50% maturity was also estimated by regressing clasper lengths on total lengths. The logistic model was transformed as:

$$CL = a' + \frac{\exp(b' + c' TL) \, d}{1 + \exp(b' + c' TL)}$$

Where CL is clasper length in millimeters, TL is total length in centimeters, and b' and c' are the intercept and slope parameters from the previous model (i.e., a and b). As to the additional parameters, a' represents the "new" intercept, and d is a scaler which allows the dependent variable to assume values outside the range 0-1, as required when proportions are considered. Least squares nonlinear regressions were fitted to the summarized maturities and clasper lengths.

The length at 50% maturity was then estimated by finding the point of inflection of the curve, given by the total length corresponding to the point where the second derivative of the function is zero, which can be found numerically.

RESULTS

Fecundity

Large variances associated with the fecundity estimates required that females be grouped by size-classes in the analyses of fecundity. Mann-Whitney U-tests on spring and autumn fecundity estimates in each 5 cm size-class were used to evaluate the null-hypotheses that the fecundities came from populations having the same mean (Table 1). H_0 is rejected if the test statistic is too large. H_0 was not rejected for all size-classes (P>>0.05) except for the 85-89 cm size-class (P<0.01). Consequently, this suggests, with some reservation, that fecundities from spring and autumn can be pooled. Given the small sample sizes from the autumn cruises, only fecundity estimates from spring were considered in the analyses by year. Data were pooled in 1980-1981, 1985-1986, 1987-1988 and 1991, and only free embryos were considered (Table 2 and Figure 1). The estimated fecundities from July through November 1942 (Templeman, 1944), July and August 1961 (Jensen, 1966), July and August 1976 (Slauson, 1982) and from the winter of 1978 (Soldat, 1979) are also given in Table 2.

Fecundity increased from 1942 to 1961 in all but the 85-89 cm size-class. An increase from 5.2 in 1961 to 6.1 in 1976 occurred in the 85-99 cm length-group. In the same period the fecundity of the 95-104 cm length-group was unchanged. The estimated fecundity for the 85-94 cm length-group in 1976 was 6.1 and in 1978 6.0, and consequently unchanged. A very clear decrease in fecundity occurred in 1980-1981,

Table 1. Results of Mann-Whitney U-tests of differences between the mean spring (S) and autumn (A) fecundities at each 5 cm size-classes. Average ranks (AR) and sample sizes (N) as well as the test statistics (Z) and probabilities (P) are shown.

Size-class	AR_S	AR_A	N_S	N_A	Z	P
80-84	33.657	32.792	54	12	-0.1373	0.8908
85-89	78.570	110.348	142	23	3.0467	<0.01
90-94	149.318	155.143	264	35	0.3801	0.7039
95-99	159.829	157.280	277	41	-0.1675	0.8670
100-104	90.220	95.086	152	29	0.4628	0.6435
105-109	18.710	17.200	31	5	-0.2775	0.7814

Table 2. Fecundity estimates from Templeman (1944), Jensen (1966), Slauson (1982) and Soldat (1979) at each 5 cm size-class (10 cm in 1976; figures from Jensen and Slauson are approximate). Estimates from 1980 and 1981 were recomputed from Nammack (1982) and all other statistics are from this study. Sample means (top), standard deviations (middle) and sample sizes (bottom) are presented. The arrows represent fecundities for 10 cm size-classes.

	1942	1961	1976	1978	1980 and 1981	1985 and 1986	1987 and 1988	1991
75-79	2.77	4.5		6.2				3.67
	0.73	—		—				1.11
	22	2		4				3
80-84	3.40	5.0		4.7	3.86	4.59	4.35	4.07
	0.88	—		—	1.35	1.37	1.58	0.96
	124	8		22	7	22	17	15
85-89	3.71	3.7	↑	5.4	5.03	5.37	4.78	4.60
	1.01	—		—	1.45	1.86	1.20	1.18
	145	6	6.1	53	31	49	45	48
			1.9					
90-94	↑	5.6	—	6.8	6.07	6.32	6.06	5.91
		—		—	1.39	1.30	1.61	1.74
	4.38	23	↓	35	141	124	77	66
	0.93							
95-99	98	7.6	↑	6.8	7.00	7.62	7.12	6.35
		—		—	1.56	1.74	1.98	1.83
	↓	13	7.7	8	147	138	94	51
			2.0					
100-104		8	—		8.33	8.67	7.84	7.09
		—			1.77	2.02	1.92	2.75
		1	↓		100	66	55	33
105-109			↑		9.50	11.2	9.67	9.22
					1.59	1.30	3.00	2.82
			9.3		16	5	12	9
			2.8					
110-114			—				8.75	
							1.26	
			↓				4	

followed by an increase to levels close to the 1978 fecundity in 1985-1986. From 1985-1986 to 1991 the fecundity decreased for all size-classes. Furthermore, fecundity increased with size in all years with the exception of the 85-89 cm size class in 1961 and the 110-114 cm size-class in 1987-1988, but in both cases the sample sizes were small. Given the apparent changes in fecundity through time, the hypothesis that these changes may be density-dependent was tested. Also, since individual fecundity is known to be a function of the volume of the female, which can be approximated by its weight, the hypothesis that fecundity changes in direct correlation with the mean weight of a mean mature female was also tested. A plot of the mean fecundities, in the periods considered above, since 1978, as well as the respective estimated indices of abundance and mean weights of the mature females (from Silva, 1993b), was made (Figure 2). In general, fecundities for all size-classes seem negatively correlated with the indices of abundance and positively correlated with the mean weights.
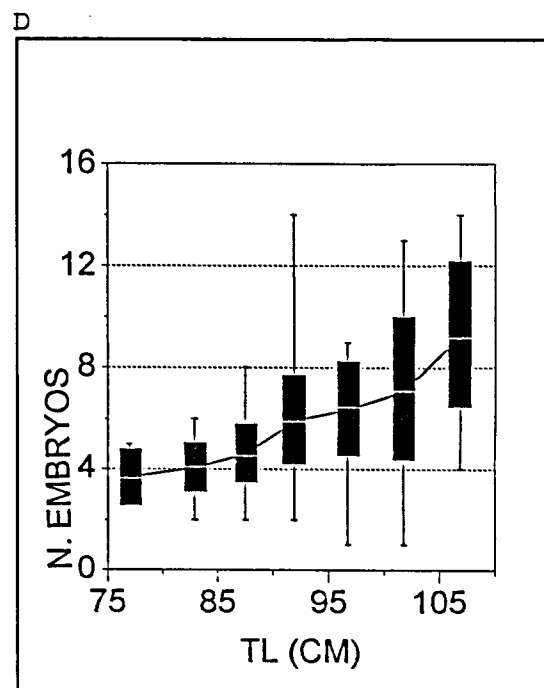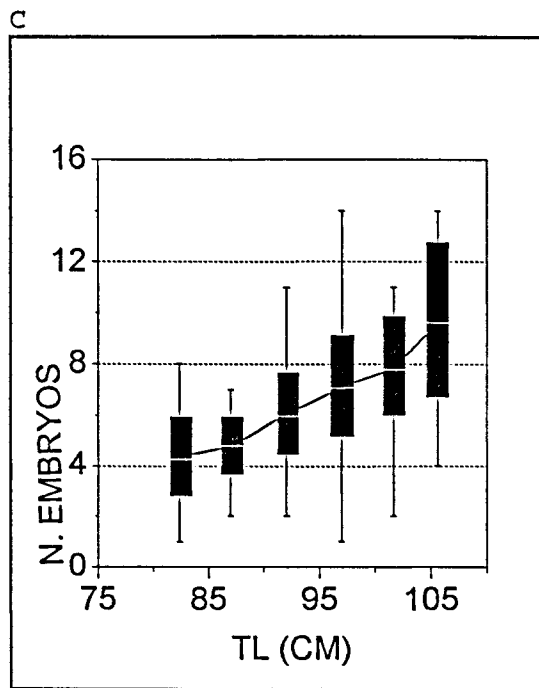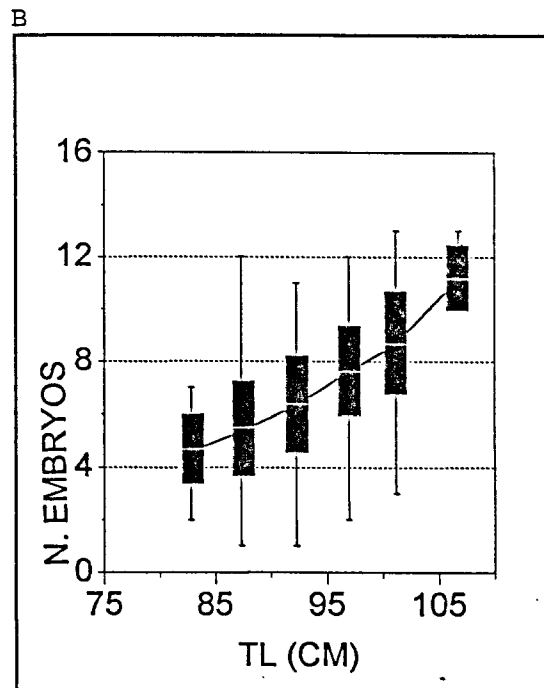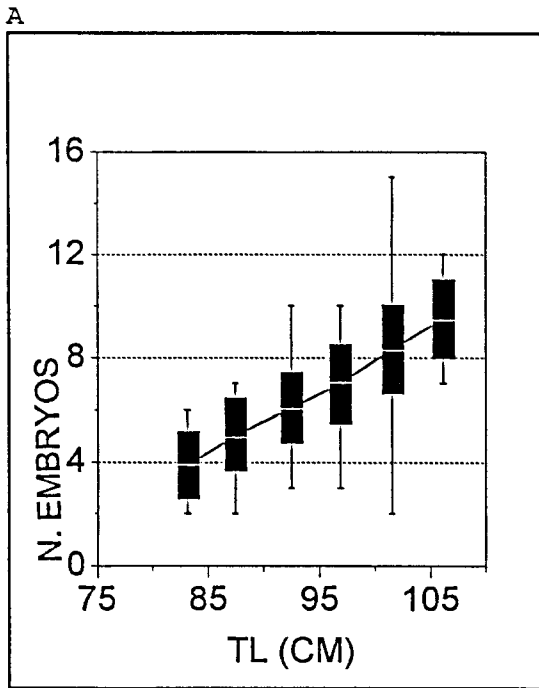
A
B

C
D

Figure 1. Changes in fecundity by size-classes from A) 1980-1981 (recomputed from Nammack, 1982) to B) 1985-1986, C) 1987-1988, and D) 1991. Depicted are the means, standard deviations and ranges.
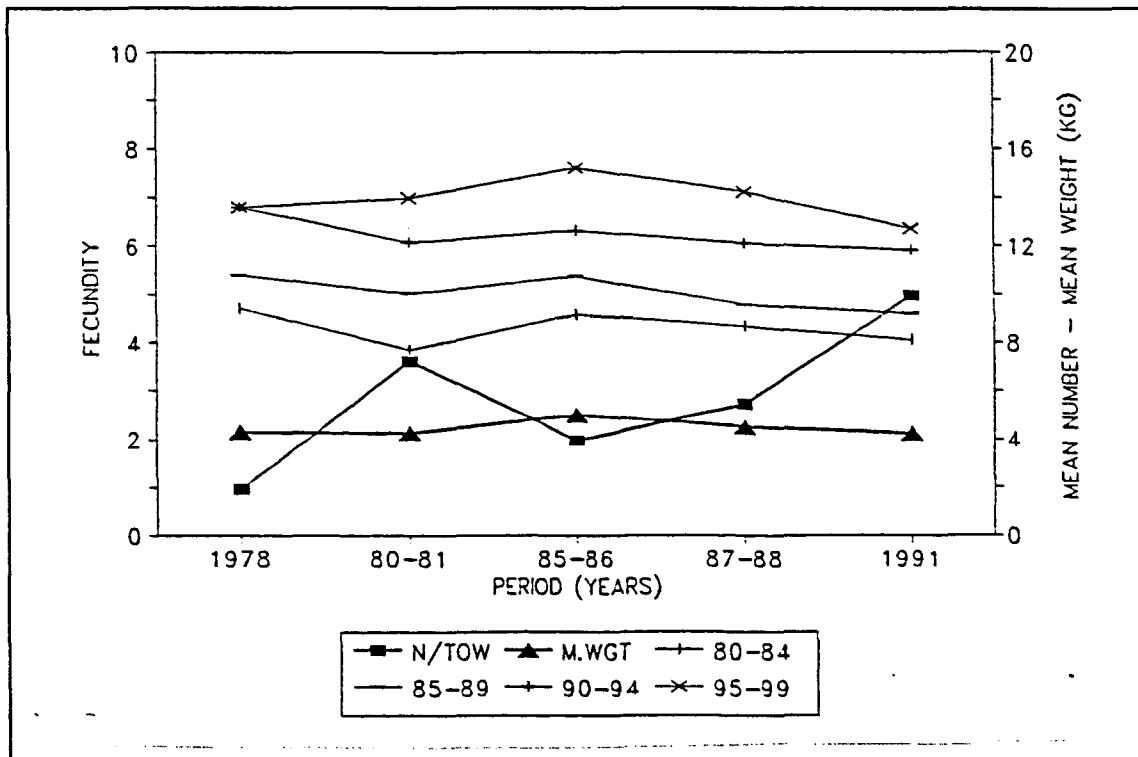
Figure 2. Mean fecundities in each size-class and respective indices of abundance and mean weights of the mature females.

Kendall's rank correlation analyses were then performed (Table 3). As expected, mean fecundities were negatively correlated with abundance indices and positively correlated with mean weights. However, while significant correlations with abundance were found for the 80-84, 85-89 and 90-94 cm size-classes ($\tau=-0.8$; P=0.05), these correlations were not significant for the 95-99 and 100-104 cm size-classes (P>0.1). The 95-99 cm size-class was significantly correlated with mean weights ($\tau=0.8$; P=0.05).

Maturity

The summarized frequencies mature at length in 1942 (Templeman, 1944) were regressed against total length using a nonlinear least

Table 3. Kendall's rank correlations, (probability levels) and number of observations (periods) between mean fecundities in each size-class (F_i) and indices of abundance of mature females ($\bar{N}$). Correlations with mean weights (W) are also shown.

	F_{80-84}	F_{85-89}	F_{90-94}	F_{95-99}	$F_{100-104}$
$\bar{N}$	-0.800 (0.0500) 5	-0.800 (0.0500) 5	-0.800 (0.0500) 5	-0.400 (0.327) 5	-0.667 (0.174) 4
W	0.400 (0.327) 5	0.400 (0.327) 5	0.400 (0.327) 5	0.800 (0.0500) 5	0.667 (0.174) 4

squares approach (the likelihood-based method could not be employed in this period since that would require that the actual observations be available, instead of the summarized frequencies mature at length). Parameter estimates and respective statistics as obtained from the analyses of female maturity in each period since 1980 using a likelihood-based method are summarized in Table 4. Figure 3 shows the fitted ogives from the logistic model. The length at 50% maturity, as estimated from the data from 1942 (80.9 cm; a=-42.3 and b=0.523), is very close to the estimate for 1980-1981 (80.6 cm). In 1985-1986 the estimated size at maturity increased to 85.9 cm and then decreased to 82.2 cm in 1987-1988. In 1991 the size at maturity increased again to 84.1 cm. The regressions were all highly significant (P>>0.05).

Size at maturity of the females and changes in the abundance of pre-adults in the period 1968-1990, as estimated by Silva (1993b), exhibited a positive relationship with the exception of the years 1988-1990, when the indices of abundance peaked at 6-11 stratified mean number per tow and the size at maturity decreased by 1 cm relative to the 1985-1986 estimate (Figure 4). The four estimates of size at maturity from the ogives fitted in 1980-1991 are also shown.

Male maturity also was inspected in the same periods except for 1987-1988 when data were too scarce to allow for maturity analysis. Length at 50% maturity was higher in 1942 and 1985-1986 (respectively 63.6 and 64.2 cm) and lower in 1980-1981 and 1991 (59.9 and 59.8 cm, respectively; Table 5). The regressions were all highly significant (P>>0.05). Templeman's (1944) data was again regressed using a nonlinear procedure instead of the likelihood-based method for the same reasons presented above for female maturity analyses. The parameter estimates were: a=-45.6, and b=0.717. However, data from Templeman (1944) can hardly be used to detect changes in size at maturity since immature fish were poorly represented in the samples. Notice that the male size at maturity changes in the same way as the female's with a sharp increase in 1985-1986 and a later decrease in 1991.

In 1980-1981 and 1991 clasper lengths were also regressed against total lengths to estimate the size at maturity. Results from these two analyses (Table 6) were very similar to the estimated sizes at maturity from the application of the maturity model and highly significant ($F_{4,\infty}0.05=2.37 \ll F$ values). The estimated size at maturity in 1980-1981 (59.5 cm) was practically the same as estimated from regression of proportion mature at length (59.9 cm). The difference between the two estimates in 1991, though small, increased to 1.0 cm. The observed and

Table 4. Parameter estimates (a and b) and associated standard errors (SE) from logistic regressions of female maturity data collected in 1980-1981 (recomputed from Nammack, 1982), 1985-1986, 1987-1988, and 1991. All data are from spring offshore cruises. Sample sizes (N), probability values associated with χ^2 goodness-of-fit tests (P>χ^2), degrees of freedom (DF) and lengths at 50% maturity (L_{50}) are also shown.

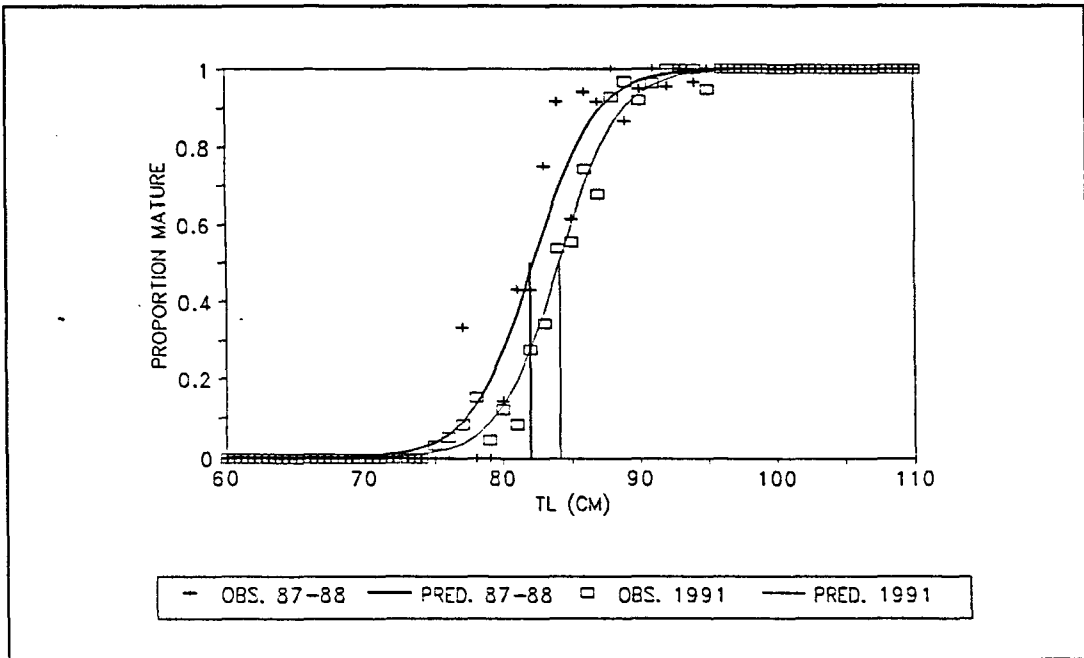| PARAMETERS	80-81	85-86	87-88	1991
N	605	700	580	999
a	-46.9	-24.4	-36.5	-38.6
SE_a	7.51	1.90	4.27	2.82
b	0.582	0.284	0.444	0.459
SE_b	0.0925	0.0215	0.0510	0.0335
DF	49	49	49	49
P>χ^2	1.000	0.930	0.997	0.999
L_{50}	80.59	85.92	82.21	84.10

A
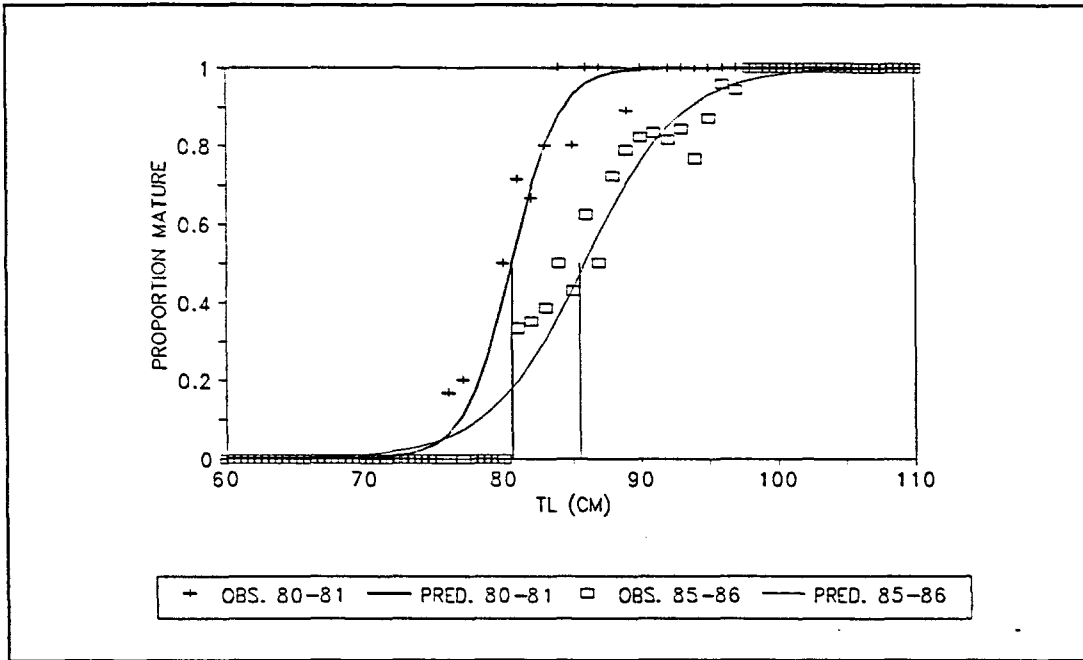
B

Figure 3. Observed proportion of mature females vs. length and fitted ogives in the periods 1980-1981 and 1985-1986 (A), and 1987-1988 and 1991 (B). Data are from spring offshore cruises only.
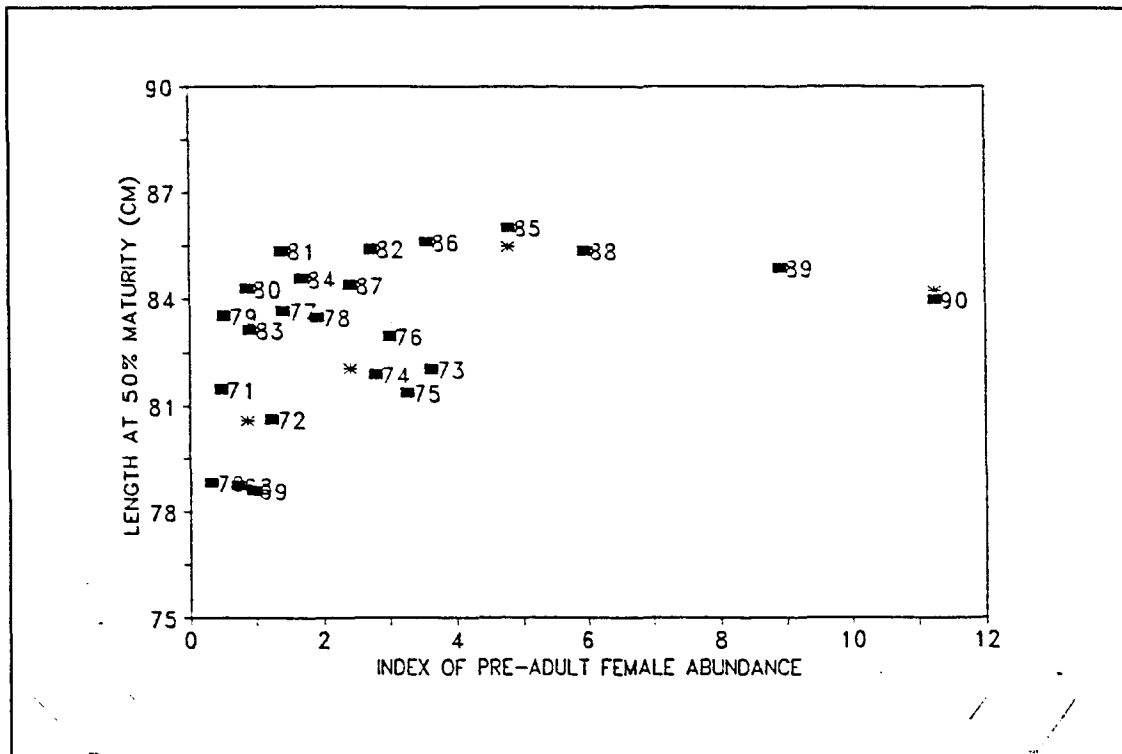
Figure 4. Size at maturity vs. pre-adult female stratified mean number per tow in the period 1968-1990 (data from Silva, 1993b). Asterisks represent these estimates from the ogives fitted in 1980-1991.

fitted maturity ogives by regression of proportion mature and clasper lengths vs. total lengths in 1980-1981 are shown (Figure 5). Figure 6 shows the maturity ogive as estimated by regression of proportion mature vs. total length in 1985-1986. The resulting fitted maturity ogives in 1991 are also shown (Figure 7).

Table 5. Parameter estimates (a and b) and associated standard errors (SE) from logistic regressions of male maturity data collected in 1980-1981 (recomputed from Nammack, 1982), 1985-1986, and 1991. All data are from spring offshore cruises. Sample sizes (N), probability values associated with χ^2 goodness-of-fit tests $(P>\chi^2)$, degrees of freedom (DF) and lengths at 50% maturity (L_{50}) are also shown.

PARAMETERS	80-81	85-86	1991
N	296	240	470
a	-59.8	-22.4	-29.0
SE_a	13.7	3.34	3.47
b	0.999	0.349	0.485
SE_b	0.2280	0.0502	0.0571
DF	39	39	39
$P>\chi^2$	1.000	0.999	1.000
L_{50}	59.86	64.18	59.79

Table 6. Parameter estimates (a-d), associated standard errors (SE), correlation coefficients, F statistics, and estimated lengths at 50% maturity (L_{50}) from logistic regression of clasper lengths vs. total lengths in 1980-1981 (recomputed from Nammack, 1982) and 1991.

PARAMETERS	80-81	1991
a	18.0	18.5
SE_a	1.24	1.26
b	-11.9	-11.9
SE_b	1.91	1.87
c	0.199	0.203
SE_c	0.0318	0.0315
d	60.7	60.2
SE_d	1.73	1.80
r^2	0.938	0.908
F	$106*10^2$	$123*10^2$
L_{50}	59.54	58.78

DISCUSSION

Several problems are associated with looking for changes in fecundity through time, particularly when estimates were obtained using different methods. A simple comparison of mean fecundities for pooled size-classes will often be meaningless since larger-sized fish will
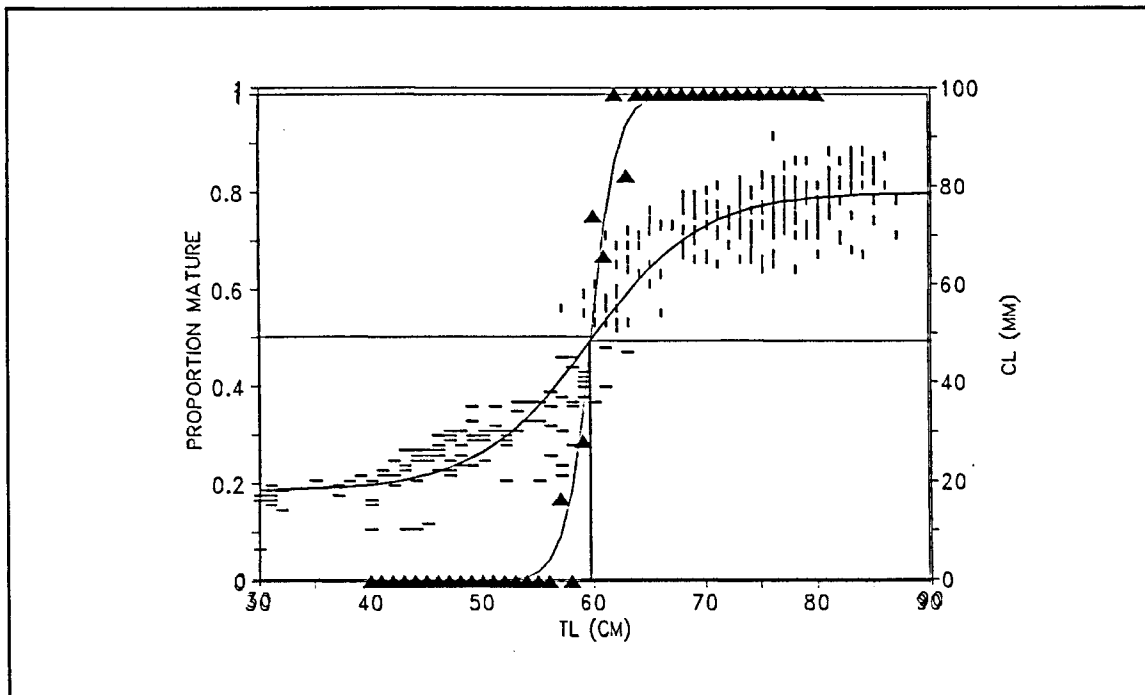

Figure 5. Observed proportion mature (triangles) and clasper lengths (horizontal bars for the immature and vertical bars for the mature fish) vs. total length and fitted ogives (light line from proportion mature and heavy line from clasper lengths). Inflection points are projected on both axes. Data are from 1980-1981.
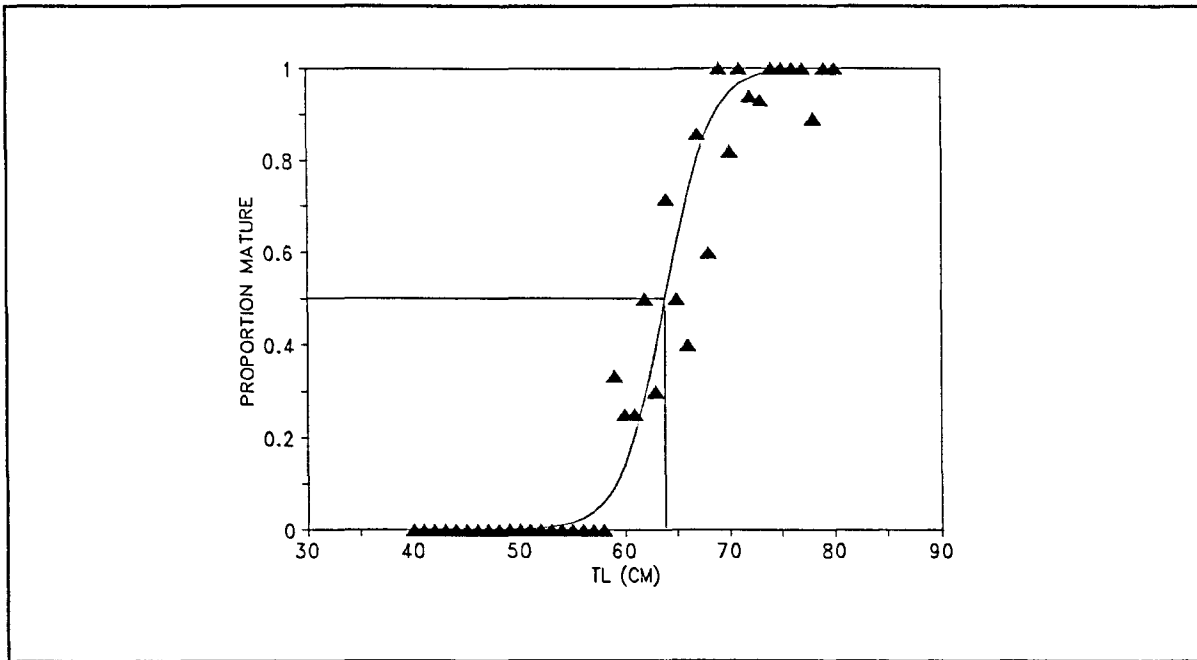
Figure 6. Observations of proportion mature vs. length and fitted ogive in 1985-1986. Depicted is the length at maturity.
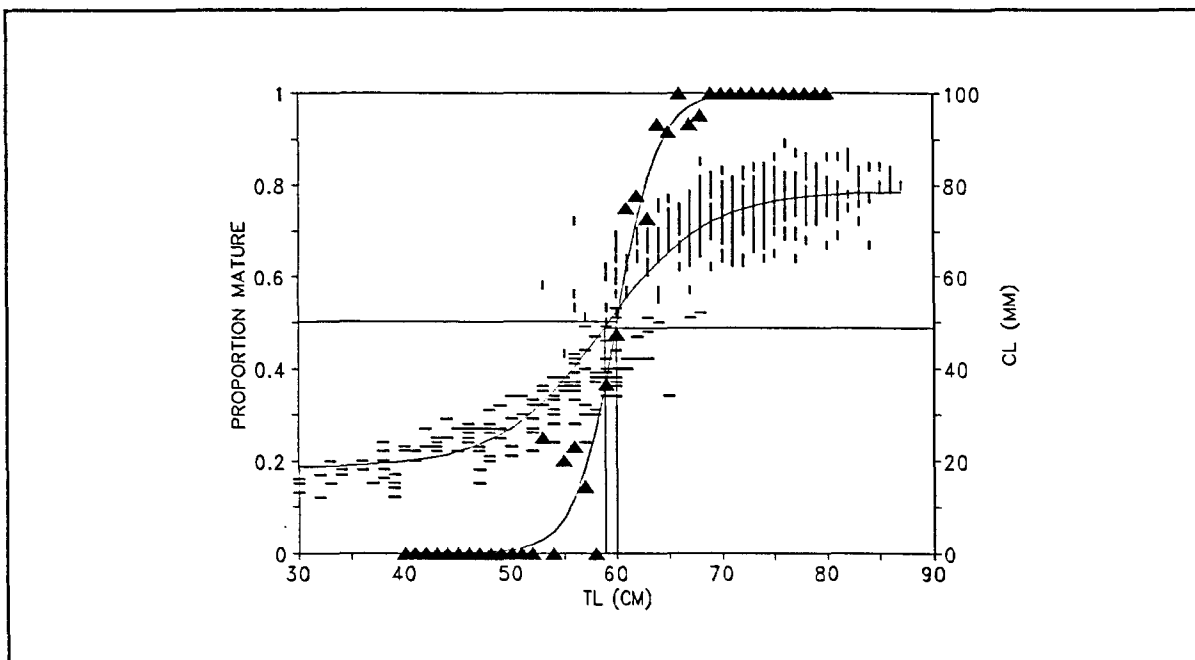

Figure 7. Observed proportion mature and clasper lengths of the immature and mature fish vs. total length and fitted ogives in 1991. Inflection points are projected on both axes.

tend to have a higher fecundity than smaller-sized fish. On the other hand, regressing fecundity on fish length, as usually done on teleosts, is not advisable since the variance associated with fecundity estimates in elasmobranchs is high. Unless size-classes are grouped in the analysis, changes will either remain undetected or spurious changes will be perceived.

Fecundity may also change with sampling site. Slauson (1982) detected an increase in the mean number of uterine embryos from 7.7 embryos per female in 1977 to 11 in 1980. Since the fecundity estimate from Nammack (1982) was considerably lower for all size-classes considered in the analysis, these differences may be due to the sample site. In fact, most of Slauson's samples came from the inshore areas around Mount Desert Island in the Gulf of Maine which may account for the higher estimated fecundity. Thus, the recomputed estimate of fecundity from 1976 (Slauson, 1982) was excluded from the density-dependent fecundity analysis.

Fecundity is usually analyzed by grouping samples by embryo size. If these sizes are not consistently chosen through time, any differences that may be detected will be hard to interpret. Templeman (1944) considered large embryos to be those "uncandled" (free embryos), usually larger than 3-4 cm. Jensen et al. (1961) and Jensen (1966) refer to the free embryos as fetuses and candled embryos smaller than 20 mm as embryos. Soldat (1979) gives fecundity estimates in terms of number of embryos but does not refer to their sizes (it was assumed that those were free embryos). Slauson (1982) separated candled embryos from free embryos in his analyses but did not report their sizes. Nammack (1982 and 1984) considered embryos larger than 9 cm as large embryos. Consequently, all embryos not classified as candles were considered free and were included in the present analysis. Moreover, since the number of candled embryos and eggs observed in this study, and in some of the aforementioned studies, were much smaller, only free embryos were included in the analyses.

Fecundity has been shown to change inversely with embryo size. Templeman (1944) reports an average fecundity (for all size-classes) of 4.2 eggs, 4.0 candled embryos and 3.7 free embryos per female, and Nammack (1984) reported 7.9 eggs, 7.4 small embryos (smaller than 9 cm) and 6.6 large embryos per female. The decreasing estimates from egg fecundity to candled embryo fecundity can be accounted for by atresia or reabsorption of the eggs. However, the more dramatic decrease from candled to free embryos is harder to explain. One explanation might be that females carrying larger embryos would be more susceptible to abortion during the fishing process, but an unreported analysis of the correlation between fecundity of females carrying large embryos and the size of the catch in an individual tow (under the hypothesis that abortion is the result of the weight of the fish in the net, in which case increased catches should result in increased rate of abortions) showed no correlation between the two variables. Moreover, if a direct relationship existed between the size of the catch and the abortion rate, the variance of the fecundity estimates should increase towards larger embryo sizes, because females carrying large embryos should be more susceptible to abort, but the opposite trend in variance has been reported (Templeman, 1944, and Nammack, 1984).

Analysis of possible differences in fecundity by size-class between samples collected in spring and autumn showed that, with the exception of the 85-89 cm size-class, no differences exist between the two groups. Since the sample sizes from autumn were small, they were not included in the analysis of fecundity. The fact that no differences exist between the two groups allowed the comparison of fecundities when samples were collected through the summer, as in the cases of Jensen (1966) and Slauson (1982), through the summer and autumn, as in Templeman's (1944) samples, or through the winter (Soldat, 1979).

13

Fecundity increased until 1976/1978. In 1980-1981 a general decrease was observed, followed by an increase again in 1985-1986. Then fecundity decreased to 1991, when it reached a level generally lower than the 1961 level. Mean fecundities and abundance are negatively correlated, whereas positive correlations were detected between fecundity and mean weight. Moreover, these correlations were significant for the 80-94 cm length-group, suggesting that the fecundity of spiny dogfish is density-dependent. The fecundity of fish in the 95-99 cm size-class, though not significantly correlated with abundance, showed a significant correlation with mean weight, suggesting that larger adult females have reduced intra-life-stage competition and consequently can allocate more energy to reproduction independently, to some extent, of their abundance.

Analyses of female size at 50% maturity showed that maturity in 1942 was achieved at a length close to the one in 1980-1981 (80.9 and 80.6 cm, respectively). Then, size at maturity increased to 85.9 cm in 1985-1986 and decreased after to 82.2 and 84.1 cm in 1987-1988 and 1991, respectively. The relationship between length at maturity, as estimated from determining the length at interception of the normalized pre-adult and adult female length frequency modes in 1968 to 1990, and the index of pre-adult female abundance were positively correlated with the exception of the period 1985 to 1990. However, it is unlikely that these changes in size at maturity represent a direct density-dependent mechanism. More likely, both variables are correlated with growth, the increasing growth rate of the juveniles during 1968 to 1979 (Silva, 1992; Silva, 1993a) resulting in increased size at maturity. Also, since growth is itself controlled in a density-dependent manner (Figure 4, from 1973 to 1984) abundance of pre-adult females should decrease. The abrupt decrease in growth rate after 1980, as a result of increased abundance during the late 1970s and 1980s, would then have the opposite effect of reducing the size at maturity some years later (Figure 4, from 1985 to 1990), i.e., length at maturity would change in a compensatory and delayed way. However, the time lag between size of the juveniles and size at maturity of that year-class, which occurs about 6 years later (in 1980-1981 the size at maturity was estimated to be 80.6 cm which corresponds to age-12, consequently there is a 6 years lag with the size of the 6-year olds in 1974) makes the analysis of correlation between the two variables hard to perform due to the way growth of the juveniles was analyzed, grouping by four-year periods. This could mean that maturity is achieved at a fixed age, with size at maturity resulting simply from the previous juvenile growth, which requires further study (see also Silva, 1993c). This would also mean that growth during the mid-late 1930s was similar to the growth observed during the mid 1970s, since the size at maturity in 1942 was close to the size at maturity in 1980-1981. However, the estimated size at maturity from Templeman (1944) should be considered carefully since the area around Newfoundland has mostly large and consequently mature fish, which may result in an overestimate.

Male size at 50% maturity shows a similar trend to the one observed in the changes in female size at maturity. Length at maturity increased from 59.9 to 64.2 cm from 1980-1981 to 1985-1986, then decreased to 59.8 cm in 1991. The estimated length at maturity in 1942 was 63.6 cm, and consequently close to the 1985-1986 estimate. However, the problem of immature fish being poorly represented is even more acute, which makes it unadvisable to include Templeman's (1944) data when looking for changing trends in size at maturity.

Clasper lengths increase rapidly at maturity (Ford, 1921). The logistic model describing the relationship between proportion mature and body length was changed to incorporate clasper length instead of proportion mature. Though two extra parameters were incorporated, making it harder to fit the model, the model can be used as either a validation tool or as an alternative to the individual classification of fish as mature or immature on the basis of the inspection of the

gonads, usually very time-consuming and imprecise. Comparison of the results obtained from the application of the clasper length model (59.5 and 58.8 cm) with those obtained from the application of the logistic model for proportion mature (59.9 and 59.8 cm in 1980-1981 and 1991, respectively) showed the differences were small.

Understanding the mechanism of fecundity regulation in fish populations is of major importance given its implications in stock-recruitment studies. Bagenal (1966) and Raitt (1968) showed that plaice and Norway pout, respectively, exhibited density-dependent changes in fecundity. These results were later corroborated for a number of other fish species (Bagenal, 1973; and, Ware, 1980). In a stable environment, a K-selected species should exhibit a negative correlation between fecundity and population density (Cushing, 1971; Mann and Mills, 1979; Adams, 1980; Pitcher and Hart, 1982). Dense populations of a long-lived fish can overcrop their food supply and selection have consequently favoured mechanisms like density-dependent fecundity, as opposed to r-selected species where population regulatory mechanisms tend to operate at a later stage through larval mortality.

Alm (1959) examined the relationship between growth and maturity in several species of fishes and suggested that as growth rates decline fish first delay maturity and mature at larger sizes, then further delay and mature at the same size and then, at very low growth rates, delay maturity even more and mature at smaller sizes. A study on the maturity of redfish in the Northwest Atlantic showed that length and age effects operate concurrently on the maturation process (Mayo et al., 1990). Other studies have aimed at improving the understanding of the interactions among life history parameters through the incorporation of a mortality cost function (Roff, 1982; Stearns and Crandall, 1984; Jensen, 1985). These works, particularly that of Stearns and Crandall (1984), have ended the disagreement over whether maturity is size- or age-driven. They concluded that it is the whole trajectory of size and age at maturity that changes under selection. Several trajectories can be perceived depending on the life-history trait of the population under study. However, when growth is not correlated with juvenile or adult mortality, as can be expected in the present case, changes in growth produce large changes in size at maturity but small changes in age at maturity, for most growth rates. Under this trajectory, large changes in age at maturity and small changes in size become apparent only at very low and very high growth rates.

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