

# GEOGRAPHIC AND HISTORIC VARIATIONS IN GROWTH OF WEAKFISH, *CYNOSCION REGALIS*, IN THE MIDDLE ATLANTIC BIGHT

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## ABSTRACT

The growth of weakfish, *Cynoscion regalis*, throughout the Middle Atlantic Bight was examined. Six geographic subdivisions were initially established for growth comparisons. Covariate analysis of the total length-scale size relationship revealed three distinct regions. Back-calculated lengths at age were compared using analysis of variance and showed significant differences between regions ( $P < 0.001$ ) and between sexes ( $P < 0.05$ ). Mean lengths at age of northern weakfish were greater than southern fish and females were larger than males after age 6. Maximum mean lengths at age were also greater in the north, 81 cm at age 11, and became progressively smaller towards the south, declining to 42 cm at age 4 in the southernmost region. The growth variations may result from varying allocations of energy to somatic growth according to environmental and migratory requirements. Growth differences resulting from the availability of food items in each habitat are also examined.

Mean and maximum lengths at age have changed over the past 50 years, with current growth greater than in 1929 or 1952. A possible relationship exists between fluctuating population sizes and historic growth variations. The current age/size structure of weakfish fisheries in Delaware Bay is discussed.

Weakfish, *Cynoscion regalis*, has been an important fishery resource within the Middle Atlantic Bight since the 19th century (Hildebrand and Schroeder 1928). In 1945, a record 41.4 million pounds of weakfish were landed by commercial interests (Wilk 1981) and, more recently, a recreational fishery has accounted for an increasing percentage of the total catch (Wilk 1981). Unfortunately, the abundance of weakfish has not always kept pace with the demand. Commercial landings totaled 27.6 million pounds in 1947 but declined thereafter, and by 1967 only 3.1 million pounds were caught. Recent landings have increased, reaching 28.7 million pounds in 1979 (Wilk 1981).

Weakfish availability to fisheries also fluctuates seasonally due to the migratory nature of the species. In April or May, weakfish migrate into estuaries to spawn (Hildebrand and Schroeder 1928) and are subjected to an inshore fishery. The migratory route is reversed in the fall, with the fish moving to warmer offshore waters (Nesbit 1954). During winter months, an offshore fishery for weakfish operates in the Virginia-North Carolina region (Pearson 1932; Jess Hawkins<sup>3</sup>).

Despite the importance of weakfish as a commercial resource, relatively little is known about the species migrations or population structure and dynamics. Previous age and growth investigations (Eigenmann 1901; Taylor 1916; Welsh and Breder 1923; Nesbit 1954; Perlmutter et al. 1956; Daiber 1957; Massmann 1963; Merriner 1973) have generally been localized studies done prior to or during the period of population decline. Following a reduction in population size, as occurred during the 1950's and 1960's, individual growth rates could theoretically be altered (Beverton and Holt 1957). Geographic variations in growth have also been suggested in previous studies, but were never examined for a single time-series of data (Perlmutter et al. 1956; Merriner 1973). This study was undertaken to assess current growth information, examine the variation throughout the Middle Atlantic Bight, and describe any long-term changes in growth that may have occurred.

## METHODS AND MATERIALS

### Sample Collection

Samples were collected by the National Marine Fisheries Service (NMFS) groundfish survey from 1979 to 1981. All weakfish were captured between Cape Fear, N.C., and Cape Cod, Mass., in depths between 5 and 200 m. Fish were collected with a #41 Yankee trawl in the spring and a #36 Yankee trawl in

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the summer and fall (Grosslein 1969). Supplemental samples were collected from May 1980 to June 1981 from commercial pound net operations in Gardiner's Bay, N.Y., and Sandy Hook Bay, N.J., and from a trawl fishery in Delaware Bay.

Weakfish from NMFS and Gardiner's Bay catches were randomly sampled and total length (TL) to the nearest millimeter (nearest centimeter for NMFS samples), sex, and maturity stage were recorded. Scales were removed from an area midway between the center of the second dorsal fin and lateral line (Perlmutter et al. 1956) on 25-30 fish per haul. Weakfish from Sandy Hook and Delaware Bays were sampled by random selection of 50-lb boxes in each size category available from the catch. Biological data and scales were collected from the subsample. Whole and gutted weights to the nearest gram were recorded for fish collected in Sandy Hook and Delaware Bays. Length-frequency data for the Delaware Bay fishery were collected by random sampling weakfish during off-loading operations in Cape May, N.J.

### Aging Methods

Impressions of nonregenerated scales were prepared on laminated polyethylene plastic and examined with a standard microfiche reader at a magnification of 32 times. Annuli were identified as the area of cutting over circuli occurring in the proximal as well as the lateral fields of the scale (Taylor 1916; Perlmutter et al. 1956). Scale measurements were made from the focus to each annulus in the lateral field and recorded directly onto ruled cards. The data were subsequently stored in an IBM<sup>4</sup> 370 computer.

### Data Analysis

To examine variations in growth, we subdivided the sampling range into geographic areas in regions and estimated growth by area. The designated regions were I, Delaware Bay to North; II, Chesapeake Bay; and III, Cape Hatteras. Six areas were established based on locations of reported spawning grounds (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953; Daiber 1957; Thomas 1971; Merriner 1976). The designated areas were 1) Cape Cod, Mass., to Block Island, R.I.; 2) Block Island to Fire Island, N.Y., which encompassed Gardiner and Peconic Bays; 3) Fire Island to Great Bay, N.J.; 4) Great Bay to Ocean City, Md., which includes Delaware Bay; 5) Ocean City to Virginia Beach, Va.,

which includes Chesapeake Bay; and 6) Virginia Beach to Cape Fear, N.C. (Fig. 1).

Back-calculated lengths at age of individual fish were calculated from scale annulus measurements using a fish TL-scale size regression equation. Individual scale measurements were adjusted according to average scale size for each fish length to reduce the variance in scale size created by scale samples not being removed from exactly the same location on each fish (Ricker 1975). Von Bertalanffy growth curves were fit to mean back-calculated lengths at age (weighted by  $n$ ) using a nonlinear regression program available in the Statistical Analysis System (Helwig and Council 1979). High correlations between  $L_{\infty}$  and  $K$  invalidated univariate

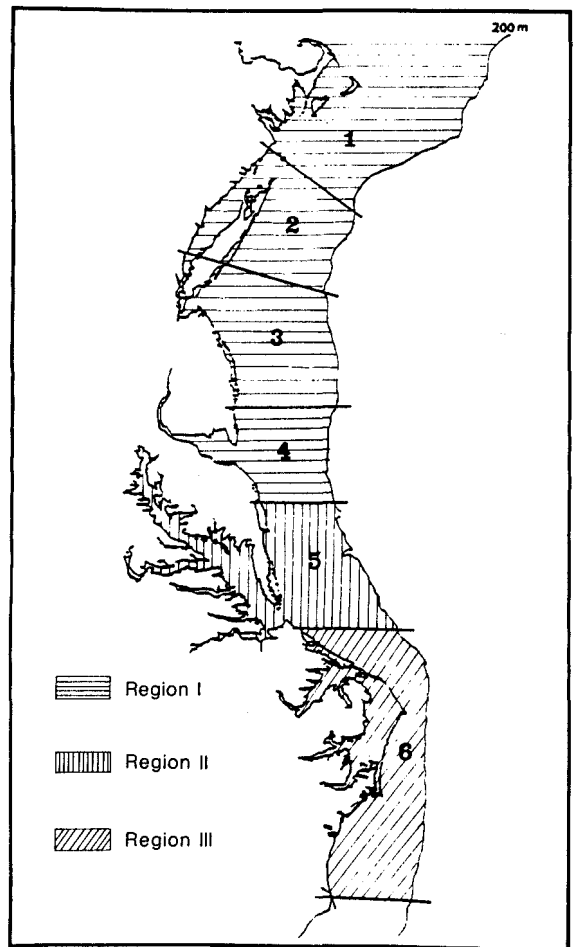


FIGURE 1.—Map of Middle Atlantic region showing stratification into three regions (I-III) and six sampling areas (1 - Cape Cod, Mass., to Block Island, R.I.; 2 - Block Island to Fire Island, N.Y.; 3 - Fire Island to Great Bay, N.J.; 4 - Great Bay to Ocean City, Md.; 5 - Ocean City to Virginia Beach, Va.).

<sup>4</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

statistical comparisons of growth curves; therefore, we compared von Bertalanffy curves following Bernard (1981). This method incorporates a Hotelling  $T^2$  test to compare matrices of parameter estimates, variances, and correlation coefficients.

## RESULTS

We made age determinations and annulus measurements on scales from 1,240 weakfish, 647 males and 593 females, ranging in size from 50 to 910 mm TL. The validity of growth rings on weakfish scales has been previously established by Taylor (1916) and Perlmutter et al. (1956). Our data show that annulus formation occurred from April to June, the point at which mean marginal increments approached minimum values (Fig. 2), which corroborates the earlier findings of annuli validity.

The relationship between fish TL (cm) and scale size (SS) per area (see Methods) was best described by a logarithmic equation. The six equations were

Area 1  $\ln TL = -1.620 + 1.054 \ln SS$   
 $r^2 = 0.874 \quad n = 23$

Area 2  $\ln TL = -1.830 + 1.117 \ln SS$   
 $r^2 = 0.956 \quad n = 132$

Area 3  $\ln TL = 0.622 + 1.073 \ln SS$   
 $r^2 = 0.958 \quad n = 171$

Area 4  $\ln TL = -2.145 + 1.178 \ln SS$   
 $r^2 = 0.879 \quad n = 524$

Area 5  $\ln TL = -1.174 + 0.971 \ln SS$   
 $r^2 = 0.857 \quad n = 190$

Area 6  $\ln TL = -0.327 + 0.785 \ln SS$   
 $r^2 = 0.639 \quad n = 200.$

The logarithmic transformation was justified following examination of the residual values (Draper and Smith 1966).

Body length-scale size regressions were compared between the six geographical areas to determine which equations should be used in back-calculating lengths at age. The equivalence of TL-SS equations between areas, sexes, and interactions was tested using analysis of covariance. Significant differences ( $P < 0.001$ ) were found in TL-SS equations between areas but not between sexes or interaction effects. Adjacent areas with similar slopes were combined into a single region. Area 1 was excluded from the analysis because of a small sample size, and the range of lengths in other areas was truncated to include equal sizes. The differences between areas were evident when the slopes of the six equations were examined (Fig. 3). Areas 2, 3, and 4 were statistically similar ( $P > 0.329$ ) and were therefore pooled into one region (Region I). Area 1 was included in the final pooled data for Region I, as the inclusion did not

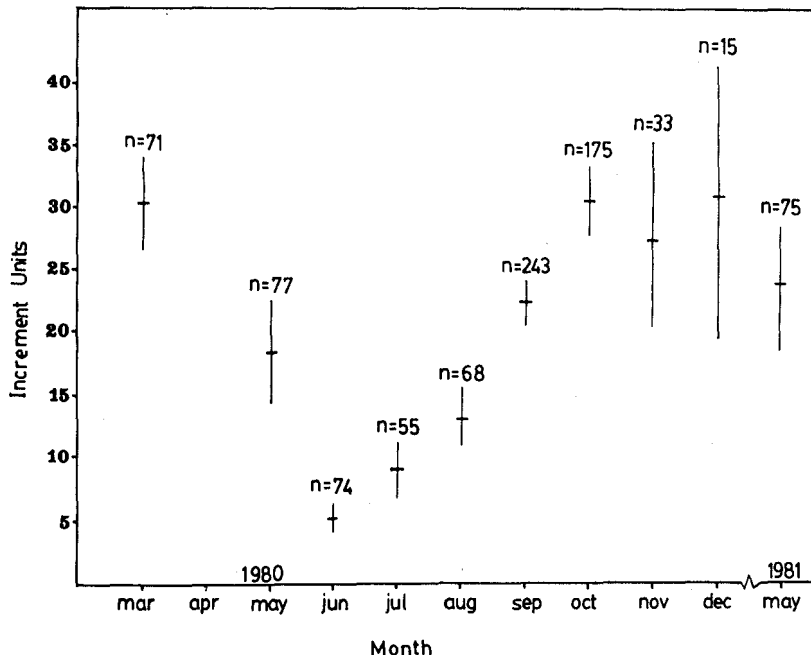


FIGURE 2.—Mean marginal scale increments  $\pm 95\%$  confidence intervals of weakfish, *Cynoscion regalis*, in the Middle Atlantic Bight for all ages combined. Sample size given for each month.

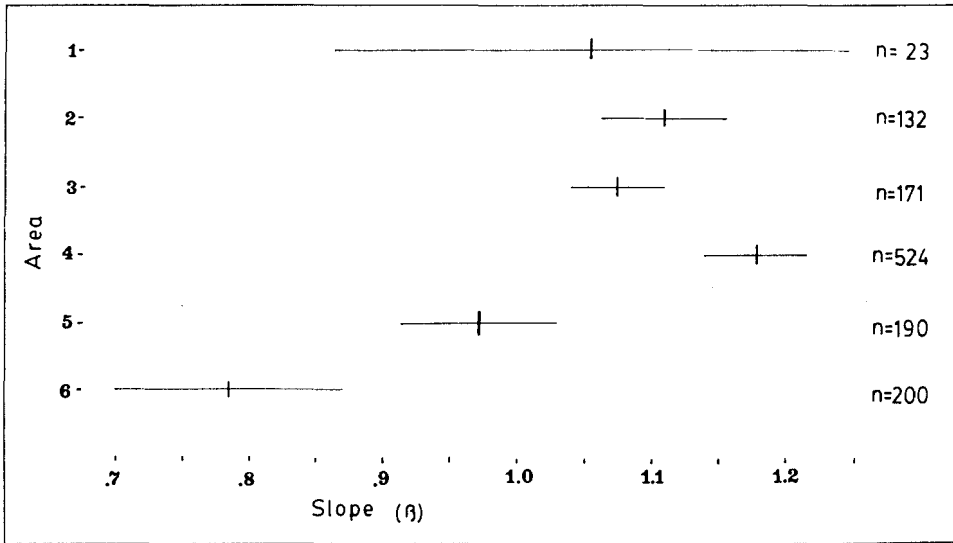


FIGURE 3.—Slopes  $\pm$  95% confidence intervals for body length (cm)—scale size regression equations of weakfish, *Cynoscion regalis*, for each area.

significantly alter the regression. Area 5 and Area 6 were each significantly different ( $P < 0.001$ ) from other equations and were thus considered separate regions. The three regional equations determined from this analysis were

$$\begin{aligned} \text{Region I} \quad \ln TL &= 1.948 + 1.139 \ln SS \\ & \text{(areas 1-4) } r^2 = 0.883 \quad n = 850 \\ \text{Region II} \quad \ln TL &= -1.179 + 0.974 \ln SS \\ & \text{(area 5) } r^2 = 0.835 \quad n = 190 \\ \text{Region III} \quad \ln TL &= -0.329 + 0.786 \ln SS \\ & \text{(area 6) } r^2 = 0.639 \quad n = 200. \end{aligned}$$

Maximum age differed substantially between regions but not between sexes. The greatest ages occurred in Region I where both sexes attained age 11. Females in Region II did not exceed age 6 while maximum age for males was age 5. In samples from Region III, the oldest age for both sexes was 4 yr.

Using the above regional equations we back-calculated lengths at age and tabulated mean lengths by sex, age group, and region (Table 1). Mean lengths for successive age groups were examined for evidence of differential survivorship, i.e., Lee's phenomena, using analysis of variance. Although a few older groups had larger size at age 1, there was no significant increase in size of the first year ( $P < 0.05$ ).

An analysis of variance (ANOVA) of back-calculated lengths at age revealed significant dif-

ferences between regions for ages 1-4 ( $P < 0.05$ ). The regions responsible for the differences were determined by Duncan's new multiple range test (Table 2). Region III fish were significantly larger ( $P < 0.001$ ) at age 1, 22 cm, compared with 20 cm for Regions I and II. By age 2, the mean length for Region I was largest, 32 cm, and significantly different from Regions II and III at 29 and 28 cm, respectively. The difference between Regions II and III was not significant. Greatest size differences existed for mean calculated lengths at age 3, between Regions I and III at 47 and 35 cm, respectively. Calculated mean length at age 4 was significantly greater in Region II than Region I ( $P < 0.05$ ), while lengths at ages 5 and 6 were not significantly different between regions.

Lengths at age were greater for females in all regions and the differences increased with age. These differences did not become statistically significant until age 6, except for 2-yr-olds in Region III where females were 3 cm larger ( $P < 0.05$ ). Region I had significant differences between sexes ( $P < 0.05$ ) for ages 6-11, except at age 9. Lengths at age 6 were 68 cm for females ( $n = 53$ ) and 66 cm for males ( $n = 39$ ); the comparison at age 11 was 81 cm for females ( $n = 3$ ) and 70 cm for males ( $n = 1$ ). No significant interactions were found between sexes and regions. Based on this analysis, length at age data were pooled for sexes in Regions II and III but separated for Region I in the subsequent fitting of growth curves.

In all three regions, the greatest growth in length

TABLE 1.—Mean back-calculated lengths at age of weakfish, *Cynoscion regalis*, by sex and region with the grand mean weighted by *n*.

Age	<i>N</i>	BCL1	BCL2	BCL3	BCL4	BCL5	BCL6	BCL7	BCL8	BCL9	BCL10	BCL11
Region I: Female												
1	57	21										
2	74	19	29									
3	97	20	33	48								
4	33	21	33	49	59							
5	18	21	34	51	60	66						
6	14	21	36	48	60	65	68					
7	13	22	35	49	60	66	70	70				
8	11	24	33	46	57	64	69	73	75			
9	6	21	30	38	49	57	63	66	69	71		
10	6	22	31	42	52	60	65	68	71	73	74	
11	3	24	30	44	53	63	69	72	74	76	78	81
$\bar{x}$	332	20	32	48	58	64	68	70	72	73	75	81
Region I: Male												
1	67	21										
2	105	19	30									
3	113	20	33	47								
4	35	19	30	46	55							
5	14	22	33	45	58	64						
6	21	20	32	48	59	65	67					
7	8	20	30	42	55	62	65	67				
8	3	22	33	45	55	60	63	66	66			
9	5	24	30	40	50	58	64	68	69	72		
10	1	20	26	42	55	59	61	64	66	69	70	
11	1	21	28	36	51	55	59	61	64	66	68	70
$\bar{x}$	373	20	31	46	56	63	66	66	68	71	69	70
Region II: Female												
1	45	19										
2	24	20	28									
3	3	23	34	42								
4	2	25	36	50	57							
5	1	22	33	45	61	68						
6	1	24	39	53	64	67	71					
$\bar{x}$	76	20	30	46	60	67	71					
Region II: Male												
1	62	20										
2	27	20	27									
3	5	23	33	47								
5	1	19	29	38	56	60						
$\bar{x}$	95	20	28	45	56	60						
Region III: Female												
1	42	21										
2	43	22	31									
3	14	21	28	37								
4	1	25	29	33								
$\bar{x}$	100	21	30	37								
Region III: Male												
1	56	22										
2	29	21	26									
3	9	23	28	32								
$\bar{x}$	94	22	27	32								

TABLE 2.—Results of Duncan's new multiple range test, including probability values, comparing mean back-calculated lengths at age of weakfish, *Cynoscion regalis*, between regions. Connecting bars indicate no significant differences ( $P > 0.05$ ); *N* is given in parentheses.

Age	Region			<i>P</i>
	I	II	III	
1	20 (752)	20 (171)	22 (194)	0.001
2	32 (615)	29 ( 63)	28 ( 96)	0.001
3	47 (408)	46 ( 12)	35 ( 24)	0.001
4	57 (212)	59 ( 5)		0.015
5	64 (147)	63 ( 3)		0.559
6	67 (112)	71 ( 1)		0.299
7	69 ( 63)			
8	71 ( 41)			
9	73 ( 25)			
10	75 ( 11)			
11	78 ( 4)			

occurred in the first year for both sexes (Table 3). Growth of weakfish from Region III was highest at 22 cm, while Regions I and II to the north each averaged 20 cm in the first year. Growth rate in Region III declined steadily after the first year. Growth in Regions I and II decreased in the second year to 10 and 7 cm, but increased to 14 and 9 cm during the third year. Thereafter growth rate declined, reaching a low of 2 cm in the 11th year for Region I and 4 cm in the 5th year for Region II.

Initial growth in weight was slower than length (Table 4). Back-calculated lengths at age were converted to weight using the GM functional regression (Ricker 1973):

TABLE 3.—True growth (cm) represented as the mean of annual increments between next-to-last and last back-calculated lengths at age for individual weakfish, *Cynoscion regalis*.

Region and sex	Age											
	0	1	2	3	4	5	6	7	8	9	10	11
I: Female	20	10	14	12	7	5	3	3	2	2	2	
Male	20	11	13	12	7	4	3	1	2	2	2	
II: Female	19	7	8	7	3	4						
Male	20	6	10	—	5							
III: Female	21	7	5									
Male	22	6	2									

TABLE 4.—Annual increments in gutted weight (g) of weakfish, *Cynoscion regalis*, by region and sex, based on the equation  $\ln \text{ gutted wt} = 4.705 + 2.984 \ln \text{ TL}$ .

Region and sex	Age											
	0	1	2	3	4	5	6	7	8	9	10	11
I: Female	80	150	634	742	603	335	241	276	248	136	478	
Male	80	172	576	584	566	326	220	227	366	122	241	
II: Female	59	119	295	508	736	481						
Male	69	100	576	714	341							
III: Female	80	163	244									
Male	92	71	92									

$$\ln \text{ gutted wt} = -4.705 + 2.984 \ln \text{ TL}$$

$$r^2 = 0.983 \quad n = 418$$

A covariate analysis indicated that the equation adequately described the length-weight relationship for both sexes ( $P < 0.001$ ). In Regions I and II, growth in weight was lowest during the first year but increased steadily reaching maximum gain at age 4, except

Region II females in which maximum weight increase occurred during the fifth year. Region III had the highest initial weight gain, but the rate of increase to maximum size, at age 3, was reduced. Annual weight increase was greater for females in Region I, although the age of maximum gain was the same for both sexes. In Region II, annual growth in weight was greater for males, but maximum growth was attained at an earlier age than for females.

Growth was described by the von Bertalanffy growth curve (Fig. 4),  $L_t = L_\infty (1 - \exp(-k(t - t_0)))$ . Parameters for the three regions are described in Table 5.

Von Bertalanffy growth curves were fit to mean back-calculated lengths for each sex in Region I and compared with the Hotelling  $T^2$  test. Differences in growth parameters  $k$ ,  $L_\infty$ , and  $w_\infty$  were not significant between sexes ( $P < 0.05$ ). The parameter  $t_0$  was significantly different between sexes ( $P < 0.05$ ), but the value of  $t_0$  is not considered biologically relevant (Galluci and Quinn 1979). Therefore, growth in Region I could be described by a single set of growth

TABLE 5.—Von Bertalanffy growth parameters for weakfish, *Cynoscion regalis*, by region.

Region and sex	$L_\infty$	$t_0$	$k$	$w_\infty$
I: Male	82.8	0.056	0.28	5.309
Female	82.3	0.005	0.26	5.202
Both sexes	82.6	0.031	0.27	5.273
II	68.6	0.051	0.35	3.026
III	40.0	-0.500	0.55	608

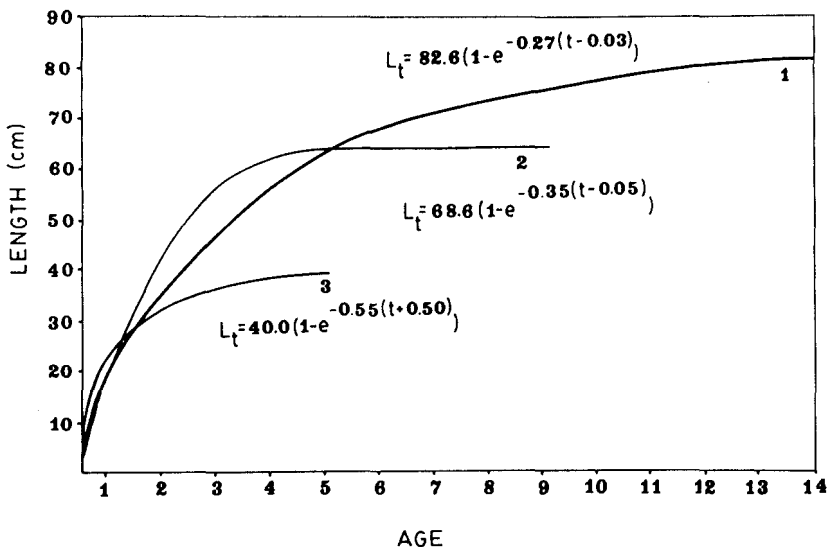


FIGURE 4.—Von Bertalanffy growth curve fitted to mean back-calculated lengths at age of weakfish, *Cynoscion regalis*, for Regions I-III (sexes combined).

parameters. No statistical comparisons of growth curves were made between regions because of the large variance around parameters in Regions II and III.

## Historic Growth

Weakfish in the New York Bight showed a general increase in length at age between 1929, 1952, and 1980-81. Back-calculated lengths at age were compared using a Student's *t*-test with variances of the 1980-81 data applied to the historic data (Table 6). The application of the 1980-81 variances to the historic data provided a more sensitive test of differences than would have been otherwise possible. Literature values (Perlmutter et al. 1956) were significantly smaller ( $P < 0.001$ ) than present mean lengths at age, with the exceptions that age 1 females and age 6 males of 1952 and age 1 males of 1929 were not significantly different from our values. After age 1, lengths at age of weakfish in 1980-81 were greater than in 1952, which were greater than in 1929. Maximum size was greatest in 1980-81 at 80 cm, followed by 64 cm in 1952 and 52 cm in 1929. Longevity was not consistent with maximum mean length at age. Weakfish in 1952 were not >6 yr old (male) while an 8-yr-old male was captured in 1929 and an 11-yr-old in 1980. Thus, larger but younger fish were caught in 1952 than in 1929, whereas 1980-81 fish were larger and older than those caught in 1929 or 1952.

## Fishery Age Structure

Age-size composition of the commercial trawl

TABLE 6.—Comparison of 1929 and 1952 growth of weakfish, *Cynoscion regalis*, in the New York Bight to 1980-81 values for each sex. Historic mean values weighted by *N*.

Age	$\bar{x}_{1929}$	<i>N</i>	$\bar{x}_{1952}$	<i>N</i>	$\bar{x}_{1980-81}$	<i>N</i>	<i>s</i>	$t_{1929}$	$t_{1952}$
<b>MALES</b>									
1	20	209	21	341	20	373	3.47	1.001	2.308*
2	26	174	28	136	31	303	6.48	8.111***	7.375***
3	30	124	36	47	46	181	6.59	27.764***	9.357***
4	32	104	48	11	56	78	5.43	29.390***	4.690***
5	36	89	56	4	63	51	4.75	32.003***	2.841**
6	41	67	64	2	66	35	3.32	36.127***	1.895
7	44	35	—	—	66	17	2.67	27.999***	—
8	52	10	—	—	68	9	2.65	12.580***	—
<b>FEMALES</b>									
1	19	190	20	401	20	332	3.53	3.427***	-0.764
2	26	172	28	115	32	269	6.87	8.799***	5.489***
3	30	132	36	49	48	187	7.15	22.148***	10.285***
4	34	114	48	13	58	95	6.07	28.505***	5.390***
5	38	91	56	5	64	63	5.43	28.899***	3.213***
6	41	56	64	1	68	50	4.47	30.922***	5.113***
7	43	29	—	—	70	31	4.51	23.543***	—
8	44	7	—	—	72	23	4.73	13.852***	—

\*\*\* significant differences  $P < 0.001$ .

\*\* significant differences  $P < 0.01$ .

\* significant differences  $P < 0.05$ .

fishery varied substantially with gear type and season. An age-length key was applied to randomly collected length frequencies to determine age structure of the fisheries in the Delaware Bay area. Spring (May-July) landings from midwater trawls consisted of fish from ages 1-10, with 85% of the catch being >55 cm and age 5. Fall catches (August-November) by otter trawls were primarily 1-yr-olds, 25-35 cm, with occasional fish as old as 7 yr (Fig. 5). Young-of-the-year fish (<20 cm) were removed from the otter trawl catches by culling. Size-frequency data of juvenile weakfish from NMFS groundfish surveys were compared with commercial fisheries data. Collections were made with otter trawls similar to those used in the commercial fisheries. The analysis of available NMFS length-frequency data was limited to areas north of Chesapeake Bay (Fig. 5). In July and August 1979, the data were primarily 1-yr-old weakfish, 20-30 cm. In September-October samples of 1978 and 1979, young-of-the-year weakfish predominated. Two length modes of young-of-the-year weakfish <20 cm were evident, undoubtedly because the juveniles were composed of individuals resulting from several spawning waves of adults (Daiber 1957; Shepherd 1982). This bimodality of juvenile lengths is reduced to a single mode by age 1, because of growth convergence or high mortality of the smaller juveniles during migration.

## DISCUSSION

Geographic variation in growth with a general tendency toward larger sizes in cooler latitudes is a common occurrence among many marine organisms (Wimpenny 1941). This phenomenon is particularly well illustrated in some marine invertebrates such as the Pacific cockle, *Clinocardium nuttalli* (Conrad) (= *Cardium corbis*) (Weymouth and Thompson 1930). Clinal variations in size have also been described for fishes such as Atlantic menhaden, *Brevoortia tyrannus* (June and Reintjes 1959), American shad, *Alosa sapidissima* (Leggett and Carscadden 1978), and croaker, *Micropogonias undulatus* (White and Chittenden 1977).

Weakfish follow a similar pattern of increasing size toward the northern end of the range. Weakfish in Region I (Cape Cod, Mass., to Ocean City, Md.) were largest at each age, and attained a greater maximum size and longevity. Growth of weakfish in Region III (Virginia Beach, Va., to Cape Fear, N.C.) was lowest, and fish from Chesapeake Bay, Region II (Ocean City, Md., to Virginia Beach, Va.), had intermediate growth. There was a discrepancy of 49 cm and 7 yr between the largest northern and southern fishes.

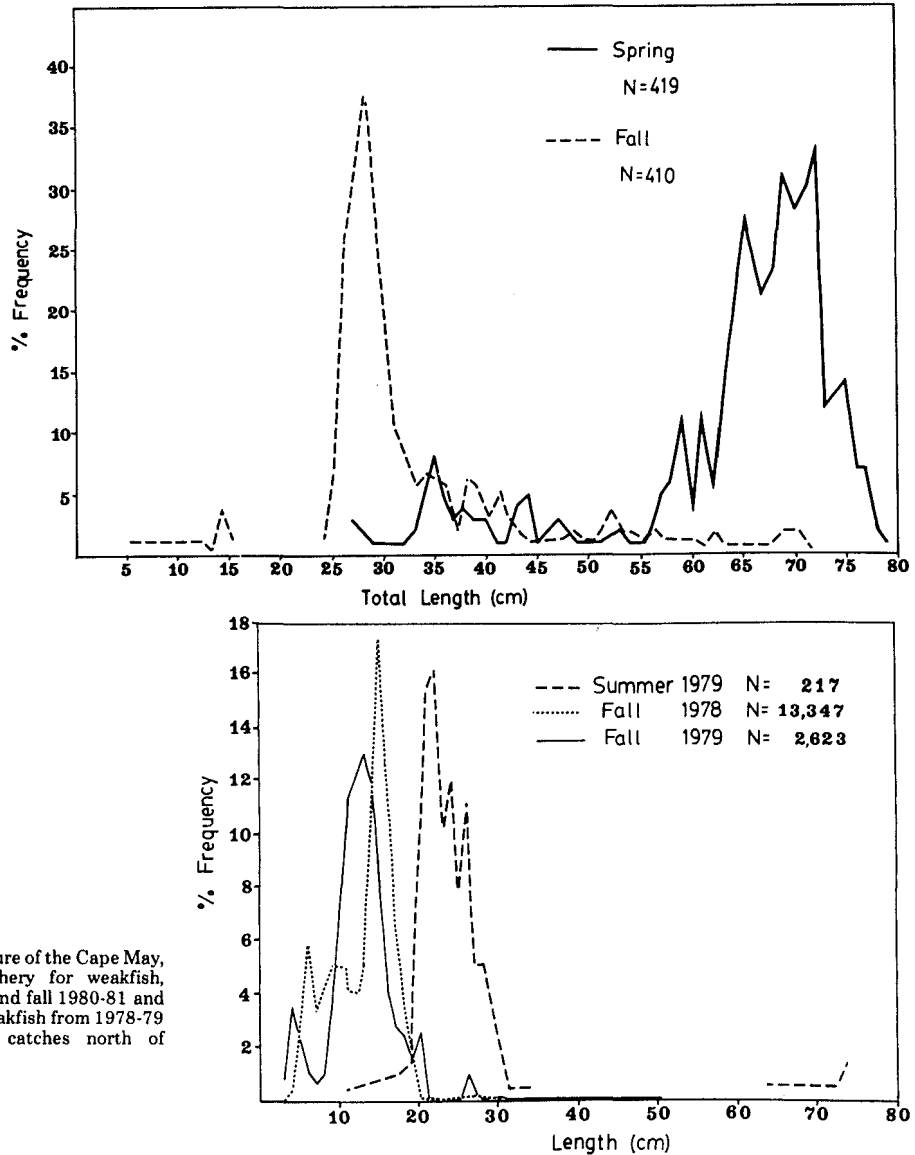


FIGURE 5.—(Top) size structure of the Cape May, N.J., commercial trawl fishery for weakfish, *Cynoscion regalis*, in spring and fall 1980-81 and (bottom) size structure of weakfish from 1978-79 NMFS groundfish survey catches north of Chesapeake Bay.

Merriner's study of weakfish (1973) in North Carolina estuaries found only small weakfish, few greater than age 4 and 44 cm which agrees well with our results. Nesbit (1954) and Perlmutter et al. (1956) also noted larger weakfish at northern latitudes.

Growth variations have been attributed to such factors as density-dependent mechanisms, temperature (Nikolsky 1963), variable energetic costs of migration and spawning (Glebe and Leggett 1981), and variable prey availability (Jones and Johnston 1977). Weakfish seasonal migrations occur in conjunction with movements of the 16°-24°C isotherms (G.

Shepherd, unpubl. data); therefore, annual variation in temperature encountered by fish in the three regions is inadequate to account for the noted growth differences. We know of no data to indicate that weakfish density varies enough between regions to create drastic growth variations by the compensatory mechanism, although the density of all fish species could be a factor.

Glebe and Leggett (1981) have shown that growth variations can result if fish in different regions are required to make varying energetic commitments between gonad and somatic growth and seasonal



migration. Presumably, seasonal migrations to take advantage of ephemeral resources (Morse 1980) must be completed in a limited time, and longer migrations would require greater energy reserves. Because swimming speed is a function of body size (Marshall 1966), larger (faster growing) fish would be better able to bear the high energy cost and complete the migration, and would thus be favored by selection. However, the penalty imposed by increased somatic growth to cope with migration would be decreased annual gonad growth and fewer gametes produced annually. Therefore, the life history strategy of migratory fish might be to assure survival by varying the energetic commitment between somatic and gonad growth according to migration cost.

These factors may explain much of the geographic variation in weakfish growth. The seasonal movements of weakfish follow a northward and inshore route in spring to spawning grounds, and feeding continues while inshore during summer and early fall before migrating offshore in mid to late fall to southern overwintering areas. The energy required for migration of northern fish to southern waters would be greatest due to the distance traveled. Therefore, northern fish emphasize somatic growth and longevity to maximize chances of surviving migration and producing gametes. Increased chances of survival for larger individuals and greater longevity result in an increased number of spawning opportunities, to offset the losses in annual gonad production. By increasing lifetime spawning frequency, this strategy has the added benefit of increasing chances for survival of gametes introduced into less environmentally predictable northern estuaries. In contrast, southern fish have little distance to migrate, so the energetic requirements for the journey are proportionately less. Because a smaller size is less of a handicap in migration, the growth strategy is shifted to increased gonad growth. This is indicated in the greater fecundities at length for southern fish (Shepherd and Grimes<sup>5</sup>). Greater emphasis on reproduction may increase adult mortality (Gerking 1959), causing the decreased longevity we observed in southern weakfish. This tradeoff between gonadal and somatic growth should not become effective until the onset of maturity. This is, in fact, the case in weakfish, as growth differences between regions become evident only after age 1, which is the approximate age at maturity (Merriner 1973). It should be noted that

the cumulative gamete production for these two life history strategies is approximately the same (Shepherd and Grimes footnote 5), thus the size differences between northern and southern weakfish do not appreciably alter the reproductive potential of the species.

Growth of southern-origin weakfish may also be limited by the availability of certain prey items. Jones and Johnston (1977) wrote that fishes pass through a series of food niches during a lifetime, and the upper limits of growth are determined in part by the optimal size for exploiting the final food niche available in a given environment. Prey availability may limit maximum size of most southern weakfish to 40-50 cm. Food habit studies by Welsh and Breder (1923) and Merriner (1975) have shown that weakfish shift prey preference to menhaden at about 35-40 cm. This size range approaches the maximum sizes of weakfish for southern waters ( $L_{\infty} = 40$  cm). Stratification of menhaden by age-size with latitude has been documented along the east coast, with 1-yr-olds predominant in the south and older, larger fish further north (June and Reintjes 1959). The implication is that net energy for southern weakfish feeding on small menhaden is insufficient for growth beyond  $\approx 40$  cm. Thus maximum size limitation of weakfish is imposed by the energy available in the final food niche. The energy saved from short migrations may be utilized to maximize reproduction before reaching the size limitations imposed by feeding. Northern fish, on the other hand, may migrate north and take advantage of a final food niche that allows superior growth.

The variations in growth may result from differences between genetically distinct groups. Our findings of three or more or less distinct body-scale relationships in Regions I, II, and III may indicate different stocks (Rojo 1977). Similar stock separations have been suggested by Perlmutter et al. (1956) and Seguin (1960). However, the body-scale relations in our study varied clinally, and such morphological characters have been shown to display clinal variation with no apparent genetic discontinuity (Katz et al. 1983). The genetic basis of these growth differences remains a topic for future research.

### Historic Variations in Growth

Weakfish populations have fluctuated widely over the last several decades, and growth rates have varied similarly, but most noticeably since the population decline of the 1960's. For example, in weakfish from the New York Bight, age 4 females in 1929 were 34 cm compared with 48 cm in 1952 and 58 cm

<sup>5</sup>Shepherd, G., and C. B. Grimes. In prep. Reproduction of weakfish, *Cynoscion regalis*, in the New York Bight and evidence for geographically specific life history characteristics. Unpubl. manusc. Rutgers University, New Brunswick, NJ 08903.

in 1980 (Perlmutter et al. 1956). Longevity has changed from 8 yr in 1929 and 6 yr in 1952 to 11 yr in 1980. Average weight per fish in recreational catches has likewise increased from 480.8 g in 1960 to 1,510.5 g in 1974 (Wilk 1979).

The trend toward increasing growth rate may be a manifestation of increased growth following the severe population decline of the 1960's. Botsford (1981) demonstrated with several species that individual growth rates will increase (compensatory growth) following a severe decline in abundance, and when the population is allowed to recover it will respond by maintaining increased growth rates and slightly lower biomass, but never regain the abundance levels experienced previous to the decline.

Present abundance of weakfish in the Middle Atlantic Bight seems to be approaching levels comparable to the predecline period of the 1950's (Murawski 1977<sup>6</sup>; Wilk 1981), while growth rates have increased over the same timespan (Table 5). These trends in abundance, the severe decline followed by a recovery, and changes in individual growth rates have followed the predicted pattern of density-induced growth compensation. Circumstantial evidence for Delaware Bay density-dependent growth changes has also been noted by Seagraves (1981).

Length-frequency data of fisheries in the Delaware Bay region suggest that current levels of exploitation may lead to decline in weakfish abundance. Commercial midwater trawl and recreational fisheries put greatest emphasis on catching the largest, and consequently the most fecund, fish during the spring fishing season. In the fall, young-of-the-year weakfish are recruited into the otter trawl fishery and constitute a large percentage of the catch, as indicated by the NMFS length-frequency data. These small fish have no market value, so are discarded from the commercial catches and likely suffer a high mortality. Therefore, fishing results in a reduction of the present and future spawning stock. It remains to be seen whether this reduction in spawning stock will cause a reduction of the weakfish population, reminiscent of the 1950's and 1960's.

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