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AGE AND GROWTH OF THE WARSAW GROUPER AND BLACK GROUPER FROM THE SOUTHEAST REGION OF THE UNITED STATES

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ABSTRACT: Opaque rings on sectioned otoliths from warsaw grouper, *Epinephelus nigritus* (N = 124), and black grouper, *Mycteroperca bonaci* (N = 172), were used to estimate age and growth. The aging structures from warsaw grouper were obtained by dockside sampling of headboat landings from North Carolina through the Florida Keys. Black grouper were sampled from headboat landings primarily in the Florida Keys. Annulus formation occurred between April and May for warsaw grouper, and from March through May for black grouper. The weight-length relationship for warsaw grouper is $W = 2.09 \times 10^{-5}L_{2.9797}$, and for black grouper is $W = 5.548 \times 10^{-6}L^{3.141}$, where W = weight in grams and L = total length in millimeters. Mean back-calculated total lengths for warsaw grouper ranged from 292 mm at age 1 to 2,328 at age 41, and from 260 mm at age 1 to 1,110 mm at age 14 for black grouper. The von Bertanlanffy growth equation for warsaw grouper is $L_t = 2,394\ (1\text{-}e^{-0.0544(t + 3.616)})$, and for black grouper is $L_t = 1,352\ (1\text{-}e^{-0.1156(t + 0.927)}$, where t = age in years and L = total length in millimeters. Both species have growth characteristics that are similar to most other serranids studied along the southeastern United States. Catch curves and a yield-per-recruit model are presented for black grouper.

INTRODUCTION

The National Marine Fisheries Service, Beaufort Laboratory, has collected biological and catch and effort data from the headboat fishery along the southeastern United States since 1972. Data from this survey have been used to estimate the age and growth of many species of reef fish (see reviews by Manooch 1982, 1987). Two species that have not been studied are the warsaw grouper, *Epinephelus nigritus,* and the black grouper, *Mycteroperca bonaci.* These species combined contribute less than one percent by weight of the annual headboat catch along the southeastern United States (Robert L. Dixon, pers. comm.), but are locally important (black grouper in South Florida), or are valued for their large size (warsaw grouper). There are no previous published results of age and growth research on these species. Studies of other groupers of the genera *Epinephelus* and *Mycteroperca* in the western Atlantic are relatively few (Manooch 1987). In this study we estimate age by examining sectioned otoliths, calculate weight-length relationships, derive theoretical growth equations for each species, and construct catch curves and estimate yield-per-recruit for black grouper.

There are two species of very large

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serranids that are occasionally caught by fishermen in the region: the jewfish, *Epinephelus itajara,* weighing up to 364 kg, and the warsaw grouper which may weigh over 200 kg. The warsaw has a wider distribution along the southeastern United States and is caught more frequently than the jewfish (Robert L. Dixon, pers. comm.). Warsaw grouper range from Massachusetts (rarely as young) to the Florida Keys, and throughout much of the Caribbean and Gulf of Mexico to the northern coast of South America. The species inhabits irregular bottom of the continental shelf break in waters 76 to 219 m deep. This habitat is characterized by steep cliffs, rocky ledges, and swift currents; it occurs 64 to 80 km off the coast of North Carolina and approximately 19 to 32 km off the east coast of Florida. Other important species of reef fish that are found in this productive, deep water zone are snowy grouper (*E. niveatus*), yellowedge grouper (*E. flavolimbatus*), tilefishes (*Lopholatilus chamelionticeps* and *Caulolatilus* spp.), and silk snapper (*Lutjanus vivanus*).

Black grouper occur off Bermuda and are distributed from southern Florida through the southeastern part of the Caribbean and West Indies to northern South America and throughout the Gulf of Mexico. Its habitat is irregular bottom such as rocky relief, coral reefs, and dropoff walls. Black grouper seem to be more closely associated with coral reefs than are the gag (*M. microlepis*) or scamp (*M. phenax*), two groupers more frequently caught by headboat anglers in the region (R. L. Dixon, pers. comm.). Young black grouper tend to occur in shallow water, whereas larger fish are restricted to depths greater than 20 m (Fischer 1978). The species is reported to attain a length of at least one meter and a weight larger than 65 kg (Böhlke and Chaplain 1968; Randall 1968; Fischer 1978).

Fishing for both species is conducted primarily by hook and line. Squid and fish baits are fished on the bottom either by single or double hook recreational rigs, or with vertical or horizontal multiple hook gear tended by commercial fishermen. Throughout much of the region the species occur as incidental catches compared with landing of other more abundant groupers.

METHODS

Sampling

Lengths and weights were recorded from 232 warsaw grouper landed by the headboat fishery (Huntsman 1976) operating along the east coast of the United States from North Carolina to Key West, Florida, 1972-1985. Size data were also obtained from 303 black grouper caught by headboat anglers, particularly in the Florida Keys, from 1977-1985.

We selected otoliths to use in estimating age and growth because grouper scales are small, deeply embedded, usually regenerated, and are thus considered of little value for age determinations (Matheson and Huntsman 1984). Otoliths (sagittae) were removed from 150 warsaw grouper and 183 black grouper either by making a cross-cut in the cranium with a hacksaw to expose the earbones, or by opening the otic bulla with a wood chisel and entering the cranium from under the operculum. The later method is easily mastered and does not deface fish that might be mounted or sold.

Otolith Analysis

Otoliths which had been dry-stored in coin envelopes in the field were shipped to the Beaufort Laboratory for analysis. In the laboratory, whole otoliths

were examined microscopically to determine if they could be read whole. Since the otoliths of both species were found to be thick and opaque, they were sectioned for age determination analysis. The plane of sectioning is of major importance to age and growth determinations. Therefore, before sectioning we examined the otoliths carefully to identify the field where rings were most legible, and where erosion of the edge was minimal. Once the cutting planes were established for both species, otoliths were sectioned with an Isomet 11-1180 low-speed saw. Three 0.3 mm sections from each otolith were submerged in clove oil in a black-bottomed watchglass and were viewed through a binocular microscope at 50X. The sections were illuminated by high-intensity, reflected light.

Opaque and dark translucent (hyaline) rings were revealed by reflected light. We hypothesized that the opaque rings represented the end of one year's growth, and therefore counted them as annuli. After enumerating the rings, we measured distances from the core to the center of each ring, from the core to the otolith edge, and from the last ring to the otolith edge with an ocular micrometer. Eighty-two percent of the warsaw otolith samples and 94% of those from black grouper could be read (rings counted), whereas 68% and 80%, respectively were legible enough to obtain measurements for back-calculating lengths at age.

Mean lengths at age for each species from all areas and years combined were back-calculated from fish length-otolith radius relationships. The prediction equations took the form: $TL = aOR^b$, where TL = total fish length and OR = otolith radius. The coefficients (a and b) were obtained by log transformation and least squares linear regression. We substituted the means of the distances from the otolith core to each annulus for OR in the above equation, calculated the mean length at the time of each annulus formation, and then calculated mean growth increment for each age group. The von Bertalanffy (1938) growth equation: $L_t = L\infty\ (1\text{-}e^{-K(t - t_o)})$, where t = age in years, $L\infty$ = asymptotic maximum length, and K = growth coefficient was fitted by the non linear least squares program BMDP-PAR (Dixon 1977). The equation was first fitted to back-calculated lengths for both species, and then to observed length at age data for warsaw grouper.

Weight-Length

We derived weight-length relationships using log transformed data and least squares linear regression for both species: $W = aTL^b$, where W = weight in grams, and TL = total length. To calculate representative relationships, we ordered fish lengths for each species separately from smallest to largest and stratified them by 100-mm intervals. All fish <500 and >1,199 mm for warsaw grouper and <400 and >999 mm for black grouper were selected because there were relatively few of them. Random subsamples for each of the other 100-mm intervals were drawn so that N for each species would equal or be greater than 100 (n per subsample $\geq$10).

Mortality

Catch curves were used to estimate instantaneous total mortality (Z) (Everhart *et al.* 1975; Ricker 1975) for black grouper. We did not use data for warsaw grouper for this purpose since they were so widely dispersed by years and geographic areas. Regressions for black grouper were fitted to the data for all ages from the modal age through the greatest age in the sample. We used the

age-length key approach to obtain age frequencies for fish from which otoliths had not been taken.

Instantaneous natural mortality (M) was estimated by using the multiple regression of M on annual mean water temperature (T in °C) and on the growth parameters K and $L\infty$ (in centimeters) (Pauly 1980-1981):

$$\log_{10} M = 0.654 \log_{10} K - 0.280 \log_{10} L\infty + 0.463 \log_{10} T.$$

Yield-Per-Recruit Model

The model for black grouper was constructed according to the methods of Beverton and Holt (1957) as outlined by Huntsman *et al.* (1983), and yield estimated by using a computer program developed at the NMFS, Beaufort Laboratory (J. Waters, pers. comm.). Instantaneous natural mortality (M) and growth parameters such as $L\infty$, $W\infty$, and K shaped the response surface, while instantaneous fishing mortality (F) and age at recruitment to the fishery (T_r) were independent variables that determined yield. Growth parameters K, $L\infty$, and t_0 were derived from the von Bertalanffy equation. Maximum age attained was considered to be 17 years noting maximum size presented in the literature, and maximum age in the fishery was determined from our basic aging data. Instantaneous natural mortality (M) was that calculated by the previously cited Pauly method.

RESULTS AND DISCUSSION

Validation of Annuli

Opaque rings on cross-sectioned otoliths from both species were considered annuli because they satisfied the criteria of Van Oosten (1929). The number of rings increased with size, age marks were consistently located on the otoliths of fish of different ages, and the otolith cross-section radius correlated well wit fish body length. The rings were forme once each year and mean back calculated lengths compared well wit mean observed lengths for most ages

Otolith cross-section radii measure ments were directly proportional to tota fish length for both species. Equation were, for warsaw grouper: $TL = 3.4780R^{1.359}$, $r = 0.94$; $N = 106$, and fo black grouper: $TL = 3.0030R^{1.324}$ $r = 0.95$; $N = 149$.

Marginal increment analysis and percentage of otolith sections with marginal rings were used to ascertain when rings were formed. In these analyses, sectioned otolith samples were grouped by month of collection and the mean distance from the last ring to the otolith edge was calculated as well as the percentage of samples with marginal rings. Opaque rings formed on otoliths of both species at about the same time of year (Figs. 1 and 2), most often from April through May for warsaw grouper, and from March through May for black grouper. Other groupers previously studied along the southeastern United States revealed the following times of annulus formation: speckled hind, *E. drummondhayi,* April through June (Matheson and Huntsman 1984); snowy grouper, May through July (Matheson and Huntsman 1984); and scamp, December through April (Matheson *et al.* 1986).

Growth

The oldest warsaw grouper we aged was 41 years and the oldest black grouper was age 14 (Tables 1 and 2). Our knowledge that slightly larger individuals of both species have been reported, leads us to believe that the maximum ages can probably be increased by 3 to 5 years.

Back-calculated total lengths for

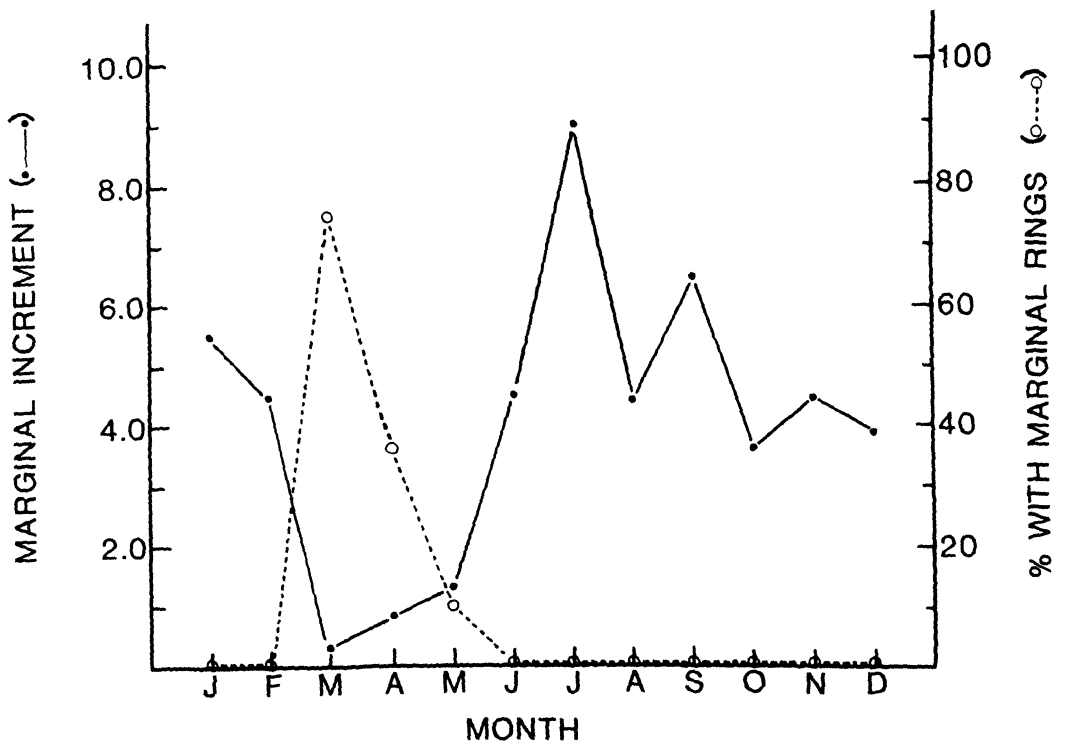

Figure 1. Time of annulus formation for warsaw grouper.

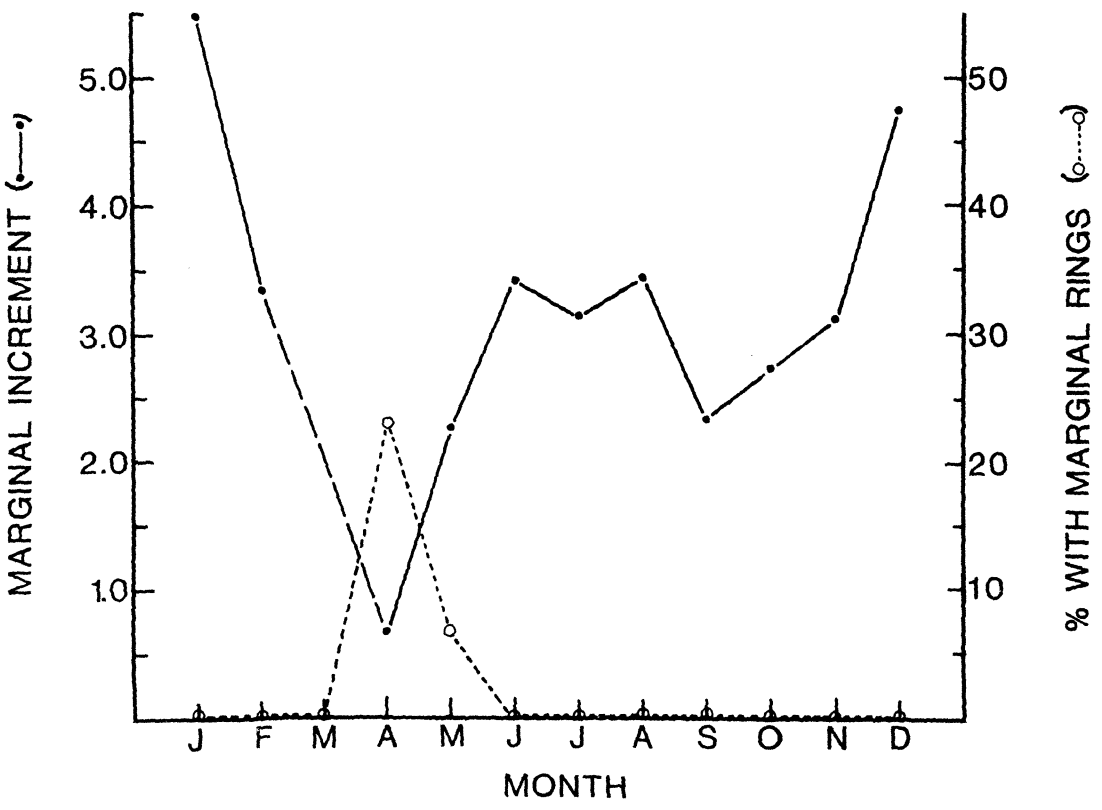

Figure 2. Time of annulus formation for black grouper. Sample size for July is one.

Table 1. Weighted mean back-calculated lengths (TL mm) at age, number of calculations, and annua growth increments for warsaw grouper.

Age	Number	Weighted mean length	Annual increment	Age	Number	Weighted mean length	Annual increment
1	103	292.2	292.2	22	2	1682.7	84.2
2	96	541.9	249.7	23	2	1725.1	42.4
3	74	703.0	161.1	24	2	1755.8	30.7
4	59	828.7	125.7	25	1	1878.9	123.1
5	36	919.9	91.2	26	1	1903.9	25.0
6	26	987.2	67.3	27	1	1954.0	50.1
7	22	1043.2	56.3	28	1	1979.2	25.2
8	20	1098.3	54.8	29	1	2017.2	38.0
9	15	1144.3	46.0	30	1	2042.6	25.4
10	13	1193.9	49.6	31	1	2068.2	25.6
11	12	1240.1	46.2	32	1	2093.7	25.5
12	10	1283.9	43.8	33	1	2119.4	25.7
13	8	1320.4	36.5	34	1	2145.2	25.8
14	6	1372.3	51.9	35	1	2171.0	25.8
15	5	1415.4	43.1	36	1	2196.9	25.9
16	3	1414.9	—	37	1	2222.9	26.0
17	3	1449.7	34.8	38	1	2249.0	26.1
18	3	1492.4	42.7	39	1	2275.2	26.2
19	3	1527.8	35.4	40	1	2301.4	26.2
20	3	1559.1	31.3	41	1	2327.9	26.4
21	3	1598.5	39.4				

warsaw grouper were 292, 920, 1,194, 1,879, and 2,328 mm for ages 1, 5, 10, 25, and 41 respectively. For black grouper, mean lengths were 260, 664, 975, and 1,110 mm for ages 1, 5, 10, and 14 respectively. Growth for both species was most rapid for the first three to four years, and then gradually trended downward throughout the remaining years of life (Tables 1 and 2). The annual growth increment of warsaw grouper for ages 24 and 25 makes an unexpected jump. We attribute this to the sample size of one used to calculate mean length: this individual is the North Carolina state record warsaw grouper and is much larger (older) than others examined in this study.

Theoretical growth equations were first fitted to back-calculated length at

Table 2. Weighted mean back-calculated lengths (TL mm) at age, number of calculations, and annual increments for black grouper.

Age	Number	Weighted mean length	Annual increment
1	146	260.1	260.1
2	144	396.9	136.8
3	130	504.1	107.2
4	118	590.8	86.7
5	98	664.0	73.2
6	74	733.9	69.9
7	51	806.1	72.2
8	25	873.1	67.0
9	14	925.1	52.0
10	8	975.4	50.3
11	5	1010.1	34.7
12	3	1054.3	44.2
13	2	1076.6	22.4
14	1	1110.3	33.6

age data. Plots of predicted variable length versus residuals and versus residuals squared, and the normal probability plot of residuals for black grouper revealed no bias. However, those for warsaw grouper data did. Therefore, we used observed length at age data to obtain a theoretical growth equation for warsaw grouper. The residuals and normal probability plot for these data revealed an acceptable fit. The von Bertalanffy growth equation for black grouper using back-calculated data was $L_t = 1{,}352(1\text{-}e^{-0.1156(t + 0.927)})$, and was $L_t = 2{,}394(1\text{-}e^{-0.0544(t + 3.616)})$ for warsaw grouper using observed data, where L_t = total fish length in millimeters at age t.

The growth coefficients for these species are similar to other coefficients obtained for groupers previously studied in the region: K = 0.179 and 0.113 for red grouper, *E. morio* (Moe 1969; Muhlia Melo 1975); K = 0.074 and 0.087 for snowy grouper (Matheson and Huntsman 1984; Moore and Labisky 1984); K = 0.122 and 0.156 for gag (Manooch and Haimovici 1978; Schlieder Unpub.[2]); K = 0.092 for scamp (Matheson *et al.* 1986); and K. = 0.100 for yellowfin grouper, *Mycteroperca venenosa* (Thompson and Munro 1974).

The asymptotic maximum lengths (2,394 for warsaw grouper and 1,352 mm for black grouper) predicted by the above growth equations seem reasonable. Black grouper are reported to attain a maximum size of 1,220 mm (Bohlke and Chaplin 1968). Of the 303 fish we examined from the headboat fishery, the three largest were 1,210, 1,240 and 1,250 mm TL. Two warsaw grouper larger than 1,830 mm (six feet) in length were sampled from the headboat fishery. These fish were 1,968 and 2,110 mm TL. In addition, a warsaw grouper weighing 190 kg (418 pounds) and measuring 2,261 mm (7.4 feet) was caught off Hatteras, NC on September 19, 1986. These large fish of both species were used in our calculations. Of those species of grouper reviewed by Manooch (1987), none were reported to attain a maximum length greater than that of warsaw grouper, and the black grouper, as reported in this study, is larger than other *Mycteroperca* groupers. Observed, back-calculated, and theoretical growth for warsaw and black grouper are depicted in Figs. 3 and 4.

Weight-Length

The weight-length relationship for warsaw grouper is $W = 2.097 \times 10^{-5}TL^{2.9797}$; r = 0.96; N = 108, and for black grouper is $W = 5.548 \times 10^{-6}TL^{3.141}$; r = 0.98; N = 101, where W = weight in grams, and length is millimeters. Using these prediction equatons, warsaw grouper 500, 800, 1,200, and 1,600 mm TL would weigth 2.3, 9.4, 31.4, and 73.9 kilograms. The North Carolina state record warsaw grouper which weighed 190 kg (418 pounds) and was 2,261 mm TL is predicted to weight 207.2 kg (456 pounds). Black grouper 400, 800, 1,000, and 1,200 mm TL are predicted to weight 0.8, 7.3, 14.7 and 26.1 kg.

Mortality Estimates

Mortality estimates may be obtained after fish have been aged and if the size or age distribution in the catch is known. If the $\log_e$ of the age frequency in the catch is plotted on age, the slope of the linear descending right limb of the curve estimates the mean instantaneous total mortality (Z). We did not attempt to estimate mortality for warsaw grouper since the size and age data were dispersed over 14 years and samples represented by many different geographical areas along the southeastern United States. We did obtain estimates of Z for black grouper since data were at

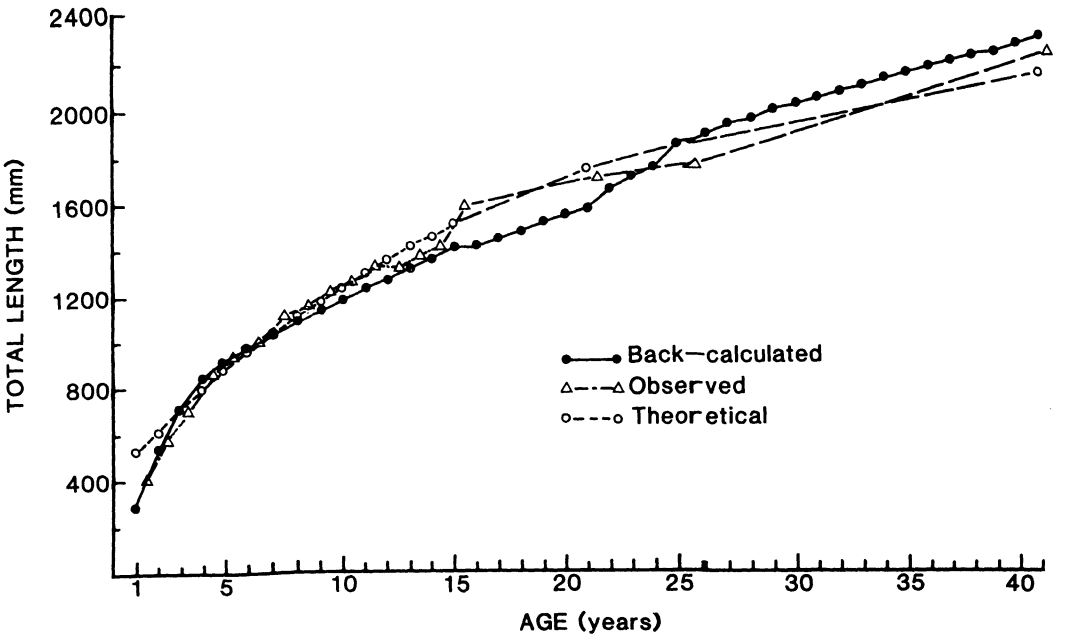

Figure 3. Growth curves for warsaw grouper.

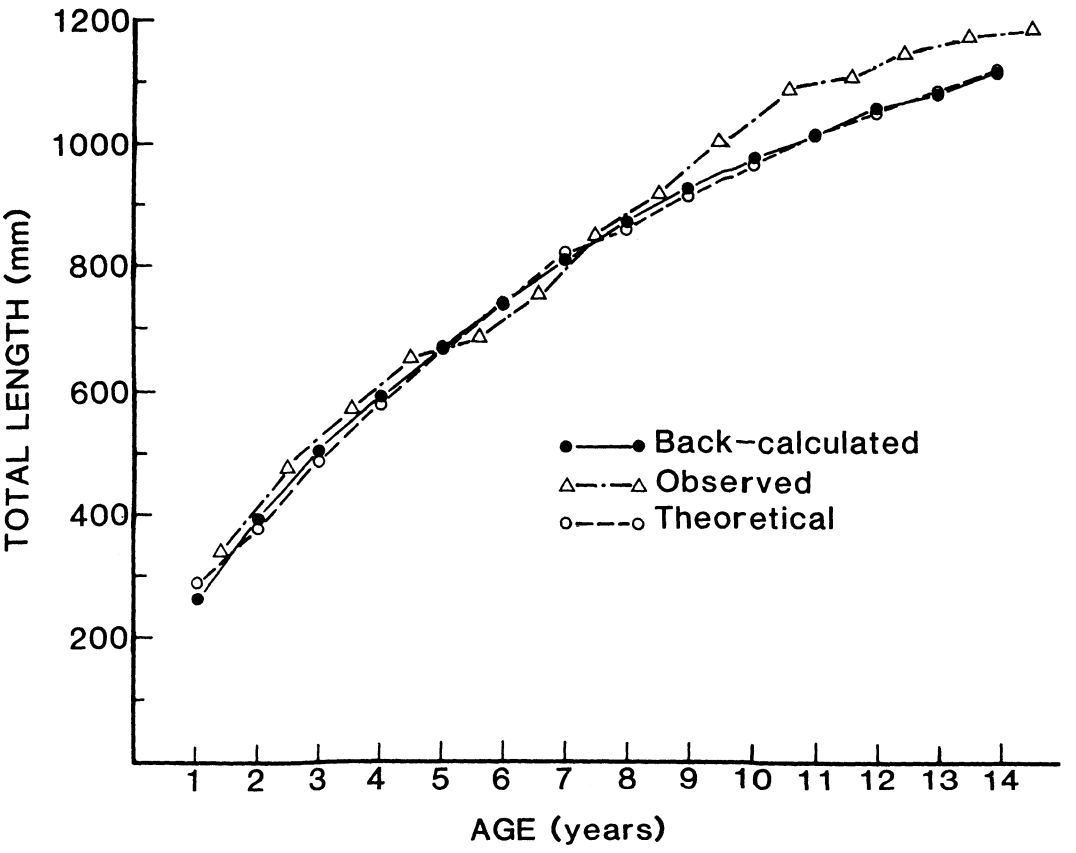

Figure 4. Growth curves for black grouper.

least concentrated by area of collection (i.e. South Florida). Determining mortality rates from the peculiarly-shaped catch curves (Figure 5) of black grouper is troubling. Several ages are almost equally frequent, and a clear downward trend in the catch curves does not appear until age six or eight depending on the curve. This same situation, apparent gradual recruitment, has been described for other *Mycteroperca* groupers (Manooch and Haimovici 1978; Matheson *et al.* 1986). Possible reasons for the almost equal representation of several ages in the catch curves may be irregular and delayed recruitment to the hook and line fishery, immigration, sampling bias, or overestimating fish ages.

Point estimates of the instantaneous total mortality rate (Z) are 0.53 based on fish aged seven and older (all years combined), and 0.49 for fish aged five and older (1981 and 1982) (Figure 5). These estimates are similar to those derived for scamp caught by the North Carolina and South Carolina headboat fishery (Matheson *et al.* 1986). If K = 0.1156, $L\infty$ = 153.2 cm, and annual mean water temperature = 26°C (averaged from data for 30 and 50 m depths in Churgin and Halminski (1974)), M = 0.28. Estimates of M for other serranids from the southeastern United States reported by Huntsman *et al.* (1983) are 0.30 and 0.50 for black sea bass, *Centropristes striatus*; 0.20 for speckled hind; 0.13 for snowy grouper; 0.20 and 0.35 for gag; and 0.17 for scamp.

Yield-Per-Recruit Model

We used the yield-per-recruit model to estimate the potential yield of black grouper. Data for warsaw grouper were inadequate for a similiar analysis. The model estimates the total weight of fish taken from a cohort divided by the number of individuals of that cohort that entered the fishing grounds.

Figure 5. Catch curves for black grouper.

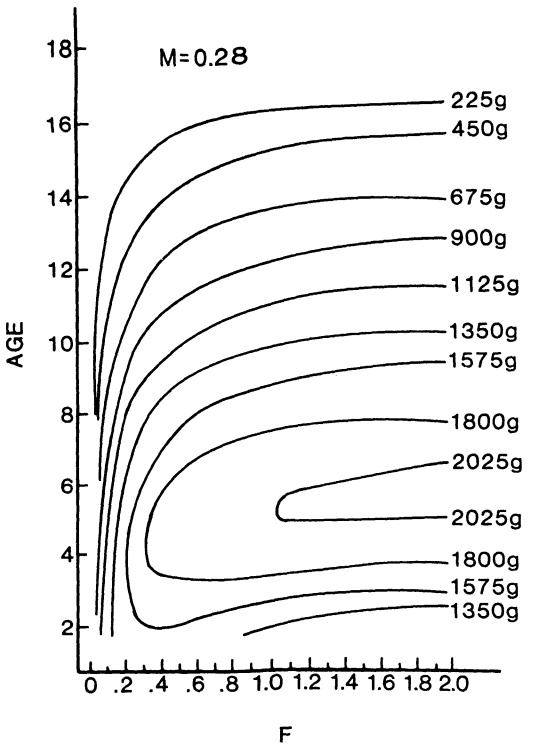

Figure 6. Yield-per-recruit model for black grouper.

The yield model for black grouper (Figure 6) suggests that South Florida headboats are harvesting approximately 67 to 78% of the potential yield at current levels of T_r (5—7 years) and F (0.21—0.25). If F is increased to 0.3 and T_r is lowered to 4.5 years, the fishery could harvest approximately 89% of the potential yield. The model for black grouper is similar to yield models developed for other reef fishes caught by headboats along the southeastern United States (see Huntsman *et al.* 1983). These authors found that for all species of reef fishes, yield-per-recruit at median recruitment ages increased rapidly in response to increasing F until F = 0.3 to 0.4. Thereafter, small increases in yield resulted from large increases in F.

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