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Age, Growth, and Mortality of Red Grouper, *Epinephelus morio*, from the Southeastern U.S.

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ABSTRACT

Sagittal otoliths, and morphometric and catch data were collected for red grouper sampled from recreational landings made in the Atlantic Ocean between Morehead City, NC and Key West, FL from 1972-1988. Rings on sagittae were determined to be annular and were legible on 461 (94%) of the sagittae examined. The oldest fish collected was 16 years and measured 866 mm total length (TL). Mean back-calculated lengths of 461 fish were 90, 240, 342, 430, 501, 560, 614, 676, 711, 736, 760, 788, 809, 819, 850, and 866 mm for ages 1 through 16, respectively. The von Bertalanffy equation (using back-calculations to the last annulus) describing theoretical growth was $L_t = 938\,(1-e^{-0.153(t+0.099)})$ where L_t = total length in mm and t = age in years. The length-weight relationship was $W = 4 \times 10^{-6}\ TL^{3.22}$ in which W = weight in grams and TL = total length in mm. Red grouper are fully recruited to the recreational headboat fishery at age 4. Instantaneous rate of total mortality (Z = 0.46) was calculated using a catch curve for all samples combined. A Ricker yield-per-recruit model suggested a maximum yield of 700 g when the instantaneous rate of fishing mortality (F) was 0.9 and recruitment age was 5.0 to 6.0 years.

INTRODUCTION

Here we determine age and growth parameters of *Epinephelus morio* (Serranidae), calculate a length-weight relationship, estimate mortality, and produce a yield-per-recruit model, using fish taken by the U.S. headboat (a boat for hire that charges on a per person basis) fleet. The biology of the red grouper has been studied in the Gulf of Mexico (Moe, 1969). The species is also an important component of the commercial and recreational reef fishery of the U.S. southeastern Atlantic coast. The red grouper attains weights of 14 kg (Smith, 1971) and ranges primarily from North Carolina to Brazil in the western Atlantic, including the Caribbean and Gulf of Mexico (Thompson and Munro, 1974). Adult red grouper occur as far north as Cape Hatteras, North Carolina. Juveniles have been recorded north to Massachusetts but are probably exported as larvae from south of Cape Hatteras by the Gulf Stream (Smith, 1971).

Red grouper are protogynous hermaphrodites, and sex reversal usually occurs between 450 and 650 mm SL (Moe, 1969), although some individuals might not undergo transformation. Sex reversal appears to be mediated by environmental conditions and social/behavioral patterns such as temperature, crowding, starvation, and sexual hierarchy (Thompson and Munro, 1974), rather than composition of the stock.

The species inhabits rocky outcrops, wrecks, and "live bottom" areas from 3 to 122 m in depth. Red grouper apparently move from shallow to deeper water (27-91 m) as they reach sexual maturity, which is at approximately age 5. Commercial fishermen allude to seasonal movement by adults to deeper offshore areas. Tagging studies showed that 10% of all tagged red grouper moved 29 km within 50 days, remaining at the same depth, while one individual moved 72 km in 466 days, moving from 31 m to 67 m (Moe, 1966).

Red grouper feed primarily on fish, crustaceans, cephalopods, and other invertebrates (Moe, 1969) and are caught commercially and recreationally by hook and line techniques (Huntsman, 1976).

MATERIALS AND METHODS

A total of 3,106 red grouper were sampled from landings of recreational headboats (Huntsman, 1976) from Morehead City, North Carolina, to Key West, Florida, 1972-1988 (Figure 1). Fish were measured for total length (mm TL) and weighed (kg) by headboat port samplers. Sagittal otoliths were removed from 488 specimens by lifting the operculum and scraping an opening in the otic bulla with a chisel. Sagittae were cleaned with distilled water, placed in a coin envelope with a collection number and morphometric data, and shipped to the National Marine Fisheries Service laboratory in Beaufort, North Carolina, for storage until samples were examined.

Whole otoliths were placed concave side up in a black watch glass containing glycerin and viewed through a dissecting microscope (12X) with an ocular micrometer (1 ocular micrometer unit = 0.83 mm) and overhead light source. Reflected light revealed two types of alternating and concentric rings: opaque rings that appeared white and translucent rings that appeared dark. As Moe (1969) found, both types were easily discernible and generally could be followed around the structure. Initially, we presumed the opaque rings to be annuli, and assigned ages (in years) to specimens equal to the number of opaque rings. We counted from the focus of the sagitta toward the anterior lateral projection, an area where rings were most legible and edge erosion was minimal (Moe, 1969).

Measurements taken were 1) focus to otolith edge (otolith radius), 2) focus to distal edge of each opaque ring, and 3) distal edge of last opaque ring to otolith edge (marginal increment). Each author made ring counts and measurements independently. If counts did not agree, the otolith was viewed again and eliminated if agreement was not reached. Of the 488 otoliths viewed, 461 (94%) were used.

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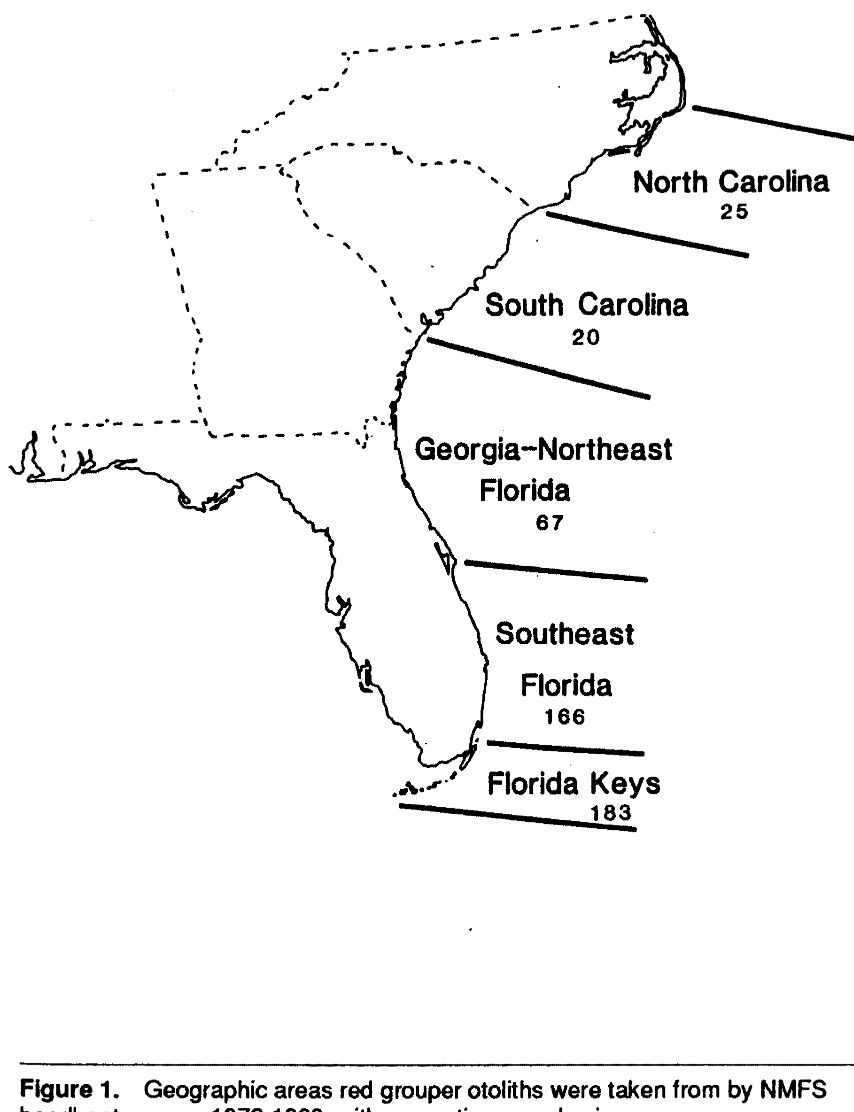

Figure 1. Geographic areas red grouper otoliths were taken from by NMFS headboat survey, 1972-1988, with respective sample sizes.

To determine if any opaque rings were occluded within the center of the sagitta, 271 otoliths were sectioned through the focus and 45° to the longitudinal axis, using a low speed saw with paired diamond-edged blades which produced a wafer 0.5 mm wide (Matheson, 1981). Sectioned otoliths were not measured but were used only as a method of comparing ages determined from whole otoliths.

Substituting the means of the distances from the focus to each annulus from samples pooled over all years and areas for OR in the equation TL = a + b (OR) in which OR = otolith radius (mm) was used to estimate mean lengths at age (Table 1). We calculated mean weighted total lengths at time of each annulus formation and mean growth increments for each age group. The von Bertalanffy (1938) growth equation $L_t = L\ (1-e^{-K(t-t_0)})$, where L = asymptotic maximum TL, t_0 = hypothetical age at which TL = is zero and K = growth coefficient, was fit to mean lengths back-calculated to the last annulus as well as to mean lengths back-calculated to all annuli with the non-linear regression program PROCNLIN (SAS Institute, 1987). A single back calculation (oldest) per individual fish avoids violation of the statistical assumption of independence among sample elements but does not necessarily provide all information available about growth of all cohorts. For comparison of results, we converted Moe's back-calculated lengths at age and asymptotic length, L , measured in standard length (SL) into total lengths using his regression equation
TL = 12 + 1.16 SL.

To determine the overall age frequencies, aged and unaged fish were grouped separately by 25-mm intervals and length groups of unaged fish were assigned to age groups in the same proportion as those of aged fish with an age-length key (Ricker, 1975). A plot of $\log_e$ catch frequency on age (Beverton and Holt, 1957) for all samples combined produced a catch curve from which we estimated Z (instantaneous rate of total mortality). We generated age-specific estimates of F (instantaneous rate of fishing mortality) using Murphy's (1965) VPA method applied to the combined fishing years 1972-1988 with an assumption of constant recruitment. Values of F for ages greater than or equal to 4 years were set equal to the value of F derived from the catch curve.

We used a yield-per-recruit (YPR) model to assess different management schemes on red grouper in the South Atlantic. The YPR is an abbreviated version of the dynamic pool model (Huntsman *et al.*, 1983) and is defined as the ratio of total weight (kg) of fish taken from a cohort divided by the number of individuals of that cohort that enter the fishery. We chose a Ricker YPR model because it allows for variable values of F and M (instantaneous rate of natural mortality) to be used and does not assume knife-edge recruitment (*i.e.*, no F until full recruitment age, full F after) as the Beverton-Holt model does. The parameters, namely, asymptotic length (L), growth coefficient (K), and ithin the center of the 45° to the longitudinal ›lades which produced hs were not measured termined from whole

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Table 1. Back-calculated mean total lengths (mm) of red grouper at time of annulus formation.

		Annuli (in yrs)															
AGE	N	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	15	144															
2	84	100	267														
3	104	78	235	349													
4	84	80	232	336	436												
5	60	72	225	330	418	505											
6	48	88	234	331	420	490	554										
7	20	119	247	348	415	479	539	593									
8	6	114	240	363	432	505	566	621	693								
9	11	120	257	380	466	527	591	637	692	729							
10	9	131	258	372	469	526	586	626	678	715	748						
11	7	93	230	323	435	514	570	613	659	696	728	757					
12	6	94	222	355	458	527	578	627	672	709	744	774	796				
13	5	71	205	333	431	493	557	610	658	694	720	750	784	811			
14	1	61	150	269	342	417	476	551	596	693	670	712	745	788	804		
15	0																
16	1	116	279	393	475	540	589	622	687	736	768	786	801	817	835	850	866
No. of back-calculations		461	446	362	258	174	114	66	46	40	29	20	13	7	2	1	1
Weighted Means		90	240	342	430	501	560	614	676	711	736	760	788	809	819	850	866
Growth Increments		90	150	102	88	71	59	54	62	35	25	24	28	20	10	31	16

theoretical age at length zero (t_0) were obtained from the von Bertalanffy growth equation while asymptotic weight (W) was calculated from the length-weight regression using L . Instantaneous rate of natural mortality (M) and growth parameters such as L , W , and K shaped the response surface, while (F) and age at recruitment to the fishery (T_r) were independent variables that determined yield.

RESULTS

Validity of Opaque Rings as Annuli

Opaque rings on otoliths met the criteria for annuli (Van Oosten, 1929). Otolith radius measurements were directly proportional to and correlated well with total length: TL = 179.7(OR) - 177, ($r = 0.94$, $N = 461$). Mean lengths at age back-calculated to the last annulus agreed reasonably well with observed mean lengths and theoretical lengths at age for most age groups as well as for mean lengths at age back-calculated to all annuli (Table 2).

A marginal increment analysis revealed the time of annulus formation and satisfied Van Oosten's requirement that annuli form yearly at approximately the same time of year. For whole otoliths grouped by month of collection, marginal increment analysis for ages 2 and 3 (Figure 2) indicated that opaque rings form April through July. Young-of-the-year fish are often used in determining approximate size at time of first annulus formation; however, fish for this study came entirely from the offshore headboat fishery, and young-of-the-year were absent. We collected one young-of-the-year red grouper by hook and line in the Newport River estuary near Beaufort, N.C. in September 1988; it measured 152 mm TL, and there was no annulus present on the sagitta.

Growth

Mean total lengths for red grouper, back-calculated to the last annulus, were 144, 267, 349, 436, 505, 554, 593, 693, 729, 748, 757, 796, 811, 804, 850 and 866 mm for ages 1 through 16 respectively, excluding age 15, for which we had no samples (Table 1). Growth in length was rapid through age 4 and then slowed. The fitted von Bertalanffy equation is:

$L_t = 938\ (1 - e^{-0.153(t+0.099)})$ (Table 3). Mean total lengths using back-calculations to all annuli were 90, 240, 342, 430, 501, 560, 614, 676, 711, 736, 760, 788, 809, 819, 850 and 866 mm for ages 1-16 respectively (Table 1). The fitted von Bertalanffy equation using mean lengths back-calculated from all annuli is:

$$L_t = 922\ (1 - e^{-0.167(t-0.299)})$$

Observed, back-calculated and theoretical mean lengths at age are compared in Figure 3.

For fish 220 to 885 mm TL, the relationship of total length to weight is: $W = 4 \times 10^{-6}\ TL^{3.22}$, $N = 427$, $r = 0.98$, where W = fish weight in grams.

Table 2. Mean observed, back-calculated, and theoretical total lengths (mm) of red grouper age 1-16.

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Table 2. Mean observed, back-calculated, and theoretical total lengths (mm) of red grouper age 1-16.

Age	N	Observed	TL Range	Back-calculated to all annuli	Theoretical	Back-calculated to last annulus	Theoretical
1	15	279	220-318	90	101	144	145
2	84	354	275-437	240	226	267	257
3	104	406	285-544	342	334	349	354
4	84	490	346-618	430	425	436	436
5	60	555	348-682	501	501	505	508
6	48	595	461-731	560	566	554	569
7	20	624	502-697	614	621	593	621
8	6	728	685-756	676	667	693	666
9	11	758	691-800	711	706	729	704
10	9	769	680-814	736	739	748	738
11	7	782	719-810	760	767	757	766
12	6	815	710-885	788	791	796	790
13	5	830	792-881	809	811	811	811
14	1	818	818	819	828	804	829
15	0	*	*	850	842	*	845
16	1	866	866	866	854	866	858

* – No age 15 fish present in samples.

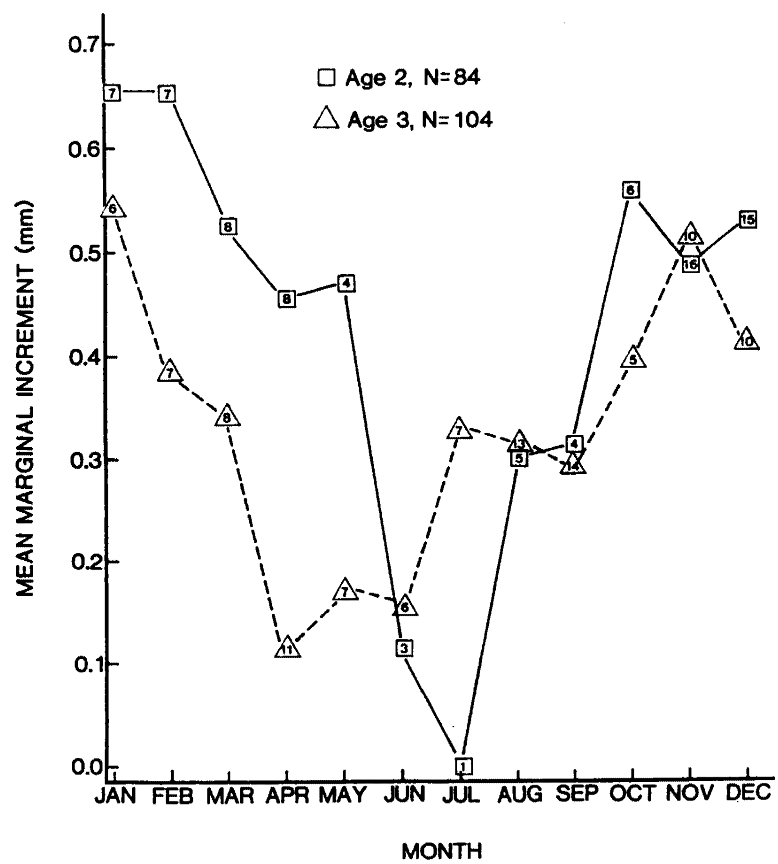
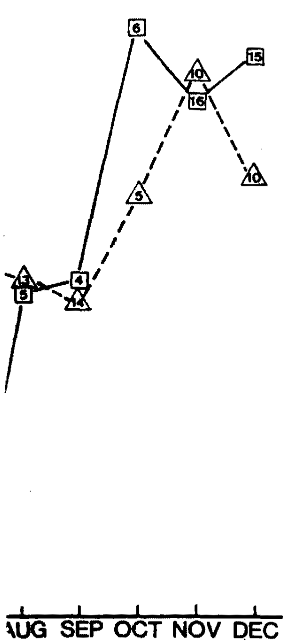


Figure 2. Mean marginal increment for whole red grouper otoliths, ages 2 and 3, by month (values enclosed are numbers of observations).



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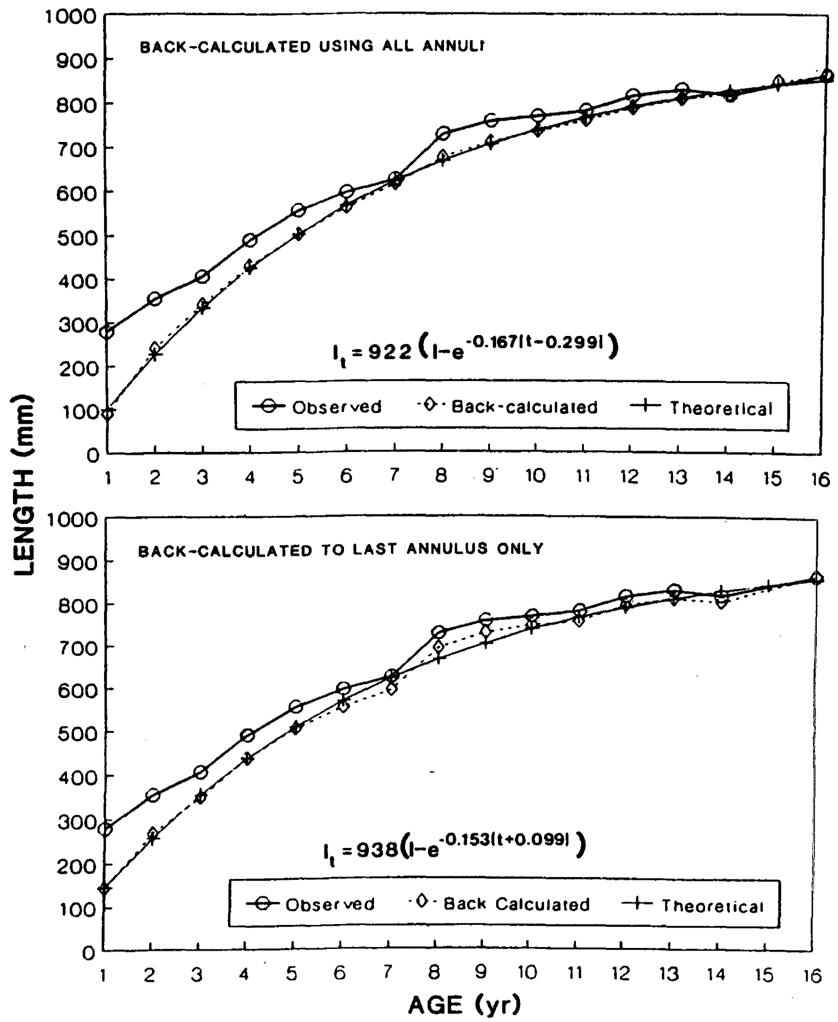

Figure 3. Mean observed, back-calculated and theoretical lengths at ages 1 to 16 of red grouper sampled by NMFS headboat survey, 1972-1988.

Table 3. Estimates of von Bertalanffy growth parameters, standard errors of 95% confidence limits for red grouper.

Parameter	Estimate	Asymptotic Standard Error	Asymptotic 95% Confidence Interval Lower	Upper
L (TL)	938	24	885	991
K	0.153	0.011	0.127	0.178
t_0	-0.099	0.152	-0.431	0.232

Lengths and weights were available for 93% of sampled fish. The others had been eviscerated prior to sampling. Length-weight relationships by sex were not calculated because the difficulty of macroscopically determining sex in these protogynous hermaphrodites precluded determining sex in the field.

Mortality

The catch curve (Ricker, 1975) ($\log_e$ frequency at age on age) (Figure 4) revealed that red grouper were not fully recruited to the headboat fishery until at least age 4, and (assuming equilibrium conditions) that Z for fish age 4 and older was 0.46 (N = 3106, r^2 = 0.96) for fish caught during 1972 - 1988. Instantaneous natural mortality (M) based on a longevity -mortality relationship (Hoenig, 1983) was 0.17. We calculated this rate using a maximum age of 25 years (Moe, 1969), corresponding to a relatively unexploited stock. Estimates of variable F at age used in the Ricker yield per recruit model were: $F_1 = 0.008$, $F_2 = 0.116$, $F_3 = 0.228$ and $F_{4+} = 0.290$.

Yield Per Recruit

A Ricker yield per recruit model (Figure 5) suggests a near-maximum yield of 1.5 kg with F = 1.08 and recruitment age between 8 and 9 years. If the entire stock of red grouper from the southeastern U.S. is subject to conditions existing under the headboat fishery (F = 0.29 and Tr = 4.0 years) then 76% of the maximum yield is currently being taken. If F were increased to 0.40 and Tr were increased to 6 years, yield could be increased to 90% of the maximum. Increasing age at recruitment while F remains constant at 0.29 will not result in a significant increase in yield per recruit. Adult F is for ages greater than or equal to 4 years, for which ages the fish are fully recruited. Values of F are lower for younger fish which are less than fully recruited.

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	Asymptotic 95% Confidence Interval	
	ower	Upper
	885	991
	.127	0.178
	.431	0.232

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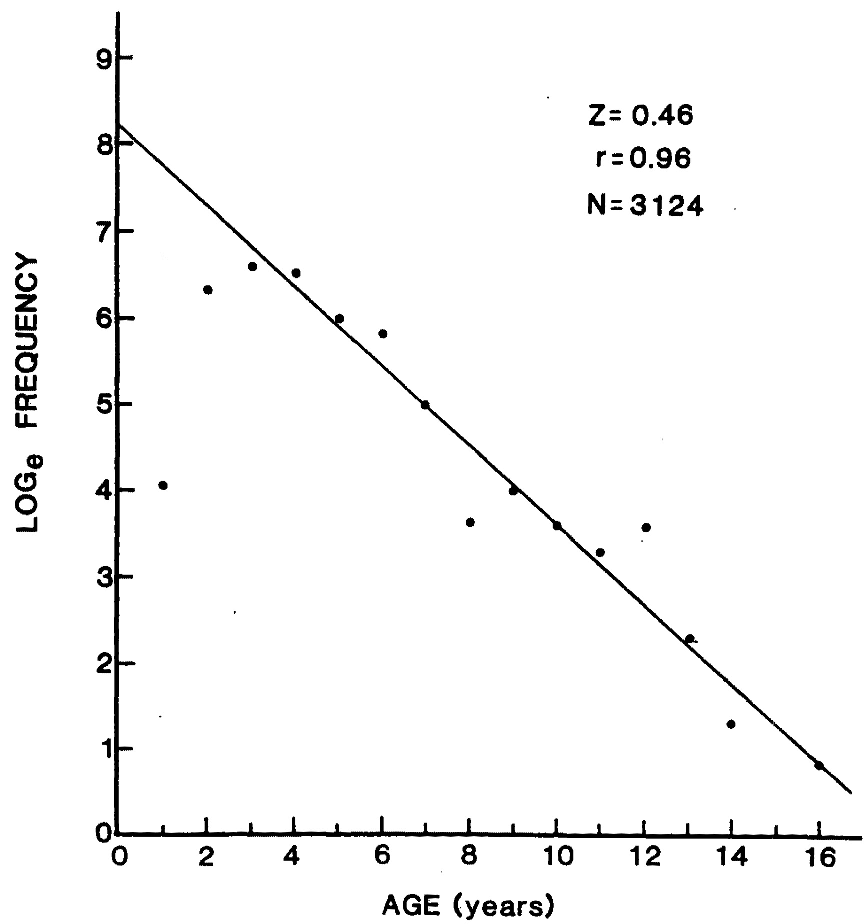


Figure 4. Catch curve for red grouper sampled by NMFS headboat survey, 1972-1988.

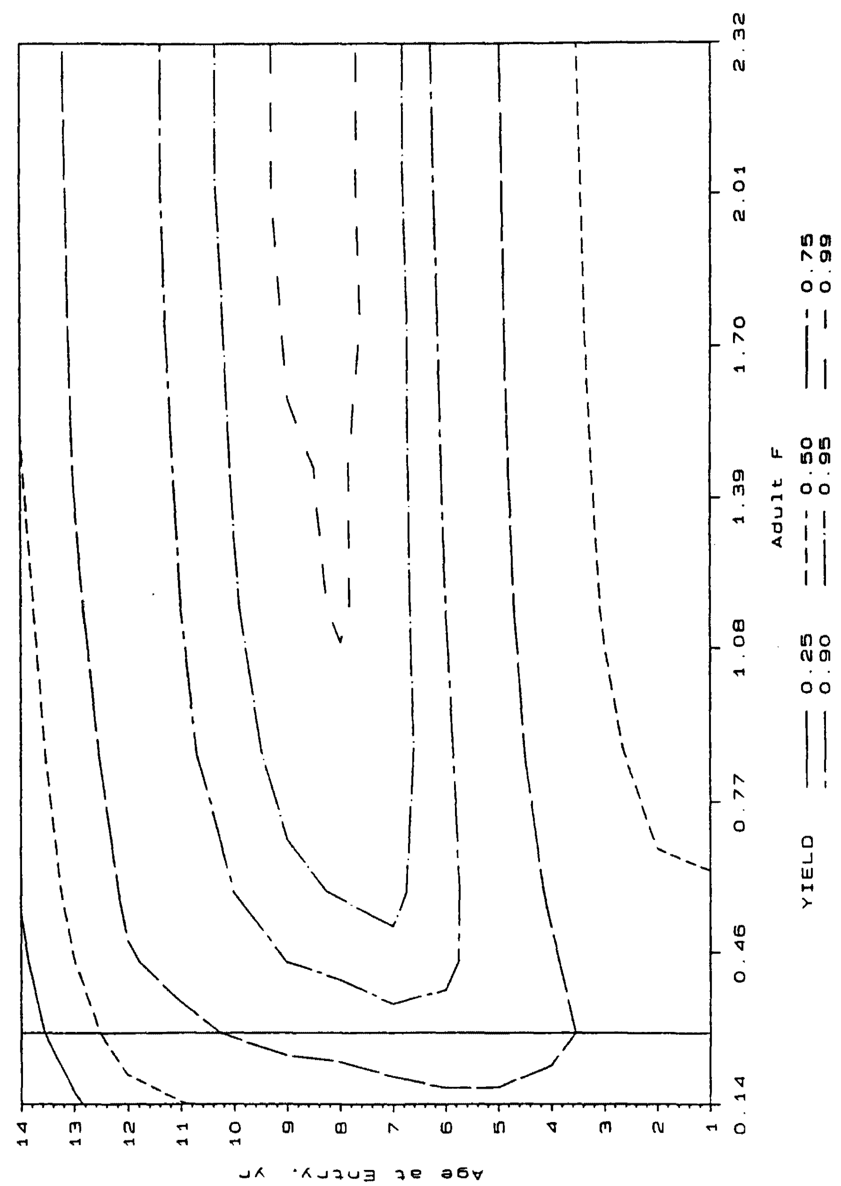
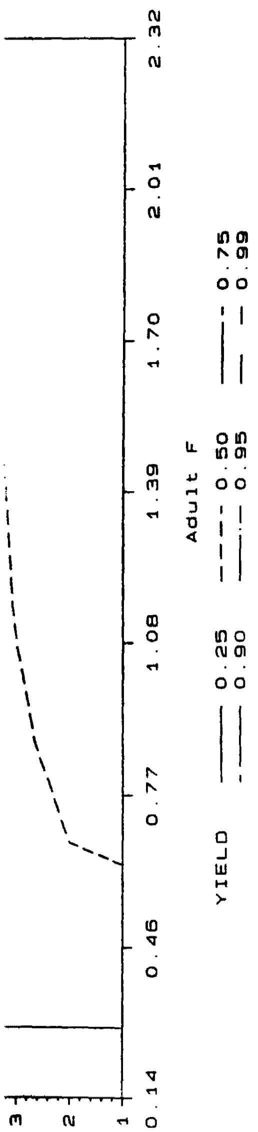


Figure 5. Ricker yield-per-recruit surface for red grouper sampled by NMFS headboat survey, 1972-1988.



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DISCUSSION

Red grouper are relatively long-lived (to age 16 or greater) with a moderate growth rate. Moe (1969) reported fish as old as age 25, although his growth equations included fish only to age 15. We suspect that the older and larger fish reported in Moe's (1969) study were acquired from commercial hook and line fishermen, a source that we did not use (hence the lack of fish older than age 16 in our study). Asymptotic length, L , for our study was 938 mm, which is substantially higher than that Moe (1969) found, L = 792 mm. Except for ages 1 through 5, when compared to Gulf of Mexico red grouper, southeastern U.S. fish tended to be larger for a given age. Back-calculated total lengths at age for red grouper from the Gulf of Mexico, ages 1 through 15, were 202, 314, 444, 491, 532, 573, 607, 637, 667, 692, 709, 723, 736 and 747 mm TL, respectively (converted to TL using Moe's SL-TL regression). Mean lengths at age of southeastern U.S. red grouper back-calculated from all annuli agree reasonably well with lengths calculated using the last annulus only for all ages except age 1 (144 mm vs. 90 mm). Back-calculated size of age 1 red grouper from our study was smaller than Moe's estimate for fish from the Gulf of Mexico (202 mm), but can in part be explained by our small sample of age 1 fish (n=15). Manooch and Haimovici (1978) found the gag (*Mycteroperca microlepis*) from the southeastern U.S. tended to be larger at a given age than those from the Gulf of Mexico.

The rate of attainment of maximum size by red grouper from the southeastern U.S., K = 0.15, is virtually the same as that found by Moe (1969, K = 0.18) for fish from the Gulf of Mexico. Red grouper from the southeastern U.S. ultimately achieve a larger maximum size than red grouper from the Gulf of Mexico. Other groupers, such as speckled hind (*E. drummondhayi*) and snowy grouper (*E. niveatus*) (K = 0.074 and 0.13, respectively: Matheson and Huntsman, 1984) and warsaw grouper (*E. nigritus*) (K = 0.054: Manooch and Mason, 1987) apparently have lower growth rates as indexed by K. Red grouper growth rates appear slightly higher than those for groupers of the genus *Mycteroperca*, gag (K = 0.122: Manooch and Haimovici, 1978) and scamp (*M. phenax*), (K = 0.092: Matheson *et al.*, 1986).

Red grouper are more common in the Gulf of Mexico. In the Atlantic they occur from Cape Hatteras to Florida but are most abundant in south Florida and the Florida Keys, the source of 76% of our samples (Figure 1).

The reef fisheries of the U.S. South Atlantic have changed dramatically in the last 15 years. The advent of sophisticated electronic gear such as high resolution depth recorders, Loran-C positioning, and electric fishing reels allows fishermen to increase effective effort (Dixon *et al.*, MS). Recreational red grouper landings and mean weights of fish from off eastern Florida have decreased in recent years (Stiles and Huntsman, MS). We suspect that exploitation of the species has reduced the chance of individuals growing to larger size. Despite increased fishing pressure, however, the red grouper appears to be maintaining mean size and abundance better than many co-occuring reef species (Plan Development Team, MS).

ACKNOWLEDGMENTS

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