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Growth and Mortality of Red Snappers in the West-Central Atlantic Ocean and Northern Gulf of Mexico[1,2]

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Abstract

Age, growth rates, mortality, and length–weight relationships were determined for red snappers *Lutjanus campechanus* from two areas in the west central Atlantic Ocean and two in the northern Gulf of Mexico. Growth rates varied only slightly among areas. The von Bertalanffy growth equation was $L_t = 975(1 - e^{-0.16(t-0.0)})$ for fish from the Atlantic and $L_t = 941(1 - e^{-0.17(t+0.1)})$ for fish from the Gulf of Mexico, where L_t is length at age t in years. The length–weight equation differed among areas, but no difference was evident between sexes. This equation for fish from all areas pooled was $W = 2.04 \times 10^{-5}\ TL^{2.953}$, where W is weight in grams and TL is total length in mm. Significant differences were found in total instantaneous mortality rates. The rate ranged from 0.39 for fish off the coast of North Carolina and South Carolina to 0.78 for fish off the coast of Louisiana. Age of full recruitment to the fishery ranged from 2 years off Louisiana to 6 years off the Carolinas.Fishing mortality appears to be the major cause of differences in total mortality among areas.

In this paper we examine annual growth, mortality, and age structure in populations of red snapper *Lutjanus campechanus* from four widely separated geographic areas. Red snappers are large, predatory fish commonly occurring in association with live-bottom and deep-reef areas from Cape Hatteras, North Carolina to the Campeche banks of Mexico. South of the Cuban Straits they apparently are replaced by the nominal congeneric Caribbean red snapper *L. purpureus*. The deep-reef habitats, essentially tropical to sub-tropical in biotic composition, are characterized by extensive algal, soft coral, and sponge growth in conjunction with bedrock outcroppings, drowned coral reefs, and other bottom irregularities (Brooks 1962; Struhsaker 1969; Smith et al. 1975; Bright and Rezak 1976). The red snapper contributes heavily to both commercial and recreational landings throughout its range (Allen and Tashiro 1976; Huntsman 1976; Nakamura 1976). Despite its value to both domestic and foreign fisheries, relatively little information is available concerning its ecology. Length–weight relationships, movements, and growth have been studied, but most work has been limited to single locations in the Gulf of Mexico, sample sizes have been small, and data virtually are absent for growth of fish older than 5 years and for mortality (Camber 1955; Dawson 1963; Moseley 1966; Beaumariage 1969; Moe 1969; Bradley and Bryan 1975; Futch and Bruger 1976; Wade 1978; Wakeman et al. 1979). Recent life-history studies of other fish in the deep-reef taxocene have been based on collections from narrow geographic ranges and do not describe the amount of geographic variation in demographic parameters—particularly growth and mortality rates—often incorporated into management models.

Methods

Red snappers were sampled between 1974 and 1979 from recreational headboat hook-and-line fisheries operating off North Carolina, South Carolina, and Florida, and from the commercial hook-and-line fishery off Louisiana. Samples were separated by geographic areas: the Gulf of Mexico off Louisiana (Louisiana); the Gulf off Panama City, Florida (West Florida); the Atlantic Ocean off Florida from Daytona south to Fort Pierce (East Florida); and the Atlantic Ocean off North Carolina and South Carolina (Carolinas). All fish were col-

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lected between June 1978 and May 1979 in Louisiana and West Florida. In East Florida, samples were taken from April 1976 to October 1978. Sampling occurred from April 1974 to November 1978 in the Carolinas.

Differences between the commerical fishery (Louisiana) and the recreational fisheries (all other areas) should be noted. Fish taken by the recreational fisheries probably were caught within 90 km of the landing port, whereas samples from the commercial fishery may have been taken 150 or more kilometers from port. Additionally, the recreational fisheries concentrate fishing pressure during the daylight hours, whereas the commercial fishery operates around the clock. Because larger red snappers may be more active during the day than smaller ones (Bradley and Bryan 1975), the recreational catch might be slightly biased toward larger fish.

Fish were measured and weighed at the port of landing, but no weights were taken in Louisiana because fish were gutted before examination. Fish sampled in the Gulf of Mexico had fork lengths (FL) recorded but those from the Atlantic had total lengths (TL) recorded. All lengths reported henceforth are TL. The relationship of FL to TL is $TL = 1.0712\ FL + 1.700$; $r = 0.99$; $N = 180$. Scales were removed from all fish. Otoliths were removed from, and sex determined for, some fish.

The 4/0 to 9/0 hook sizes commonly used in all fisheries tended to exclude fish smaller than 180 mm from the catch. However, 263 small red snappers were obtained from research trawling off the Carolinas and in Saint Andrews Bay in West Florida through the courtesy of the South Carolina Marine Resources Research Institute, Charleston, and the National Marine Fisheries Service, Panama City, Florida.

Scales were taken from beneath the tip of the posteriorly extended pectoral fin, stored in paper envelopes, cleaned, rinsed, and dried before being read and measured. They were examined by eye and with a hand lens for signs of regeneration and potential legibility. If available, four scales from each fish were mounted on glass slides and viewed on an Eberbach[3] projector at 27× magnification. All measurements were taken along the anterior radius of the magnified image from the focus to each observed ring.

Otoliths (sagittae) were exposed by a transverse cut with a hacksaw through the cranium midway between the posterior edge of the orbit and the preopercle. They were removed with forceps and stored in paper envelopes. All otoliths were sectioned laterally through the focus with a Buchler Isomet 11-1180[3] low-speed saw by procedures of Berry et al. (1977). Sections of 0.18 to 0.28 mm thickness were mounted on glass slides with Permount[3], and projected and viewed in the same manner as scales. All measurements were taken from the focus to each observed ring along the medioventral ridge.

Scales and otoliths from all fish less than 235 mm and greater than 800 mm were used, because both size extremes were infrequently encountered. The commonly sampled sizes were divided into 50-mm length classes and subsampled. All scales and otoliths were read at least twice at an interval of 2 or 3 months. Those from fish greater than 800 mm were read three times, and either the mode or the mean was used as estimated age.

Rates of instantaneous total mortality (Z) were estimated by the regression method (Ricker 1975) and the method of Robson and Chapman (1961). Instantaneous rates of natural mortality (M) were determined with the procedure described by Pauly (1980). An estimate of the instantaneous rate of fishing mortality (F) was obtained by subtraction: $F = Z - M$ (Ricker 1975).

Results and Discussion

Validity of Age Determination

Scale samples from 2,151 fish representing all study areas were examined and 76% were usable. On legible scales, recurring patterns of compressed circuli in conjunction with marked crossing over of circuli in the lateral fields were consistently evident. We hypothesized that these compressed circuli were annuli and took measurements from the focus to the midpoint of each. Circuli were quite close together in recent annuli of the largest fish and exact determination of the number of annuli became increasingly difficult as fish lengths exceeded 850 mm.

Otoliths from 142 red snappers collected off the Carolinas were examined and 90% were legible. Left and right otoliths from eight ran-

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

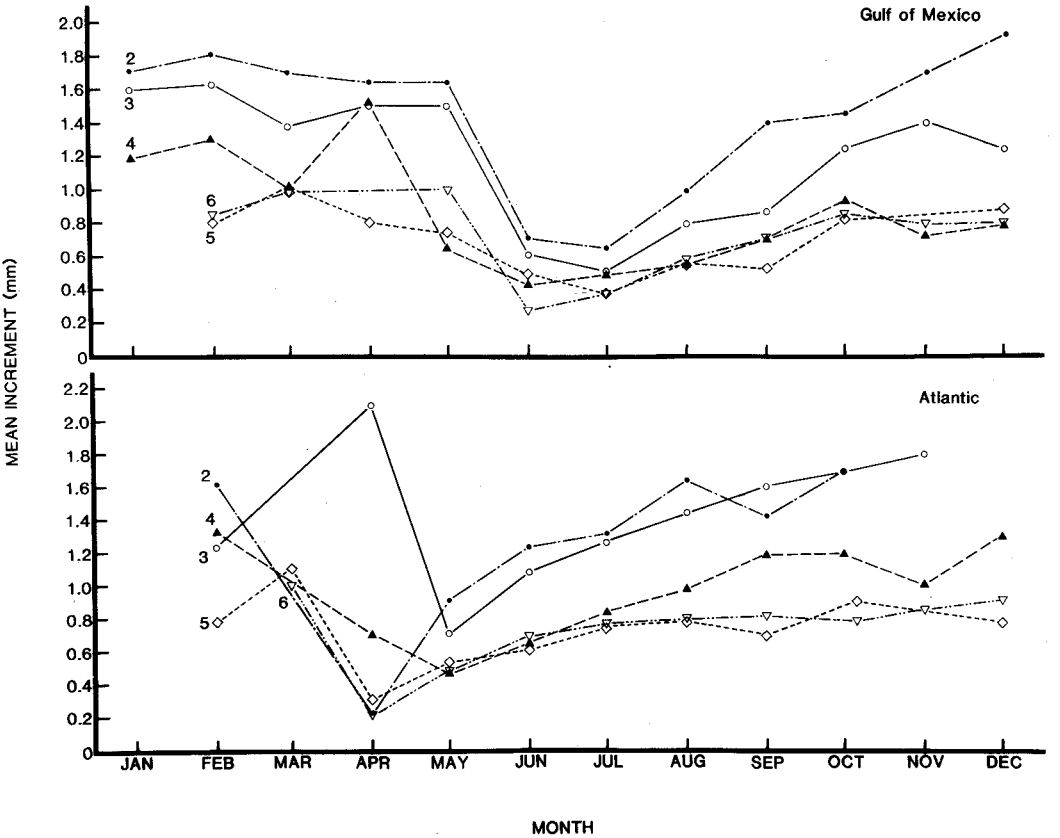

FIGURE 1.—*Mean monthly scale increment for red snappers aged 2 to 6 years collected in the Atlantic Ocean (1974–1978) and the Gulf of Mexico (1978–1979). The April increment for 4-year-old red snappers is a single observation.*

domly selected fish of 53 to 523 mm were read independently and agreed; thereafter we sectioned only the left otolith from the remaining fish. Otolith sections viewed in transmitted light contained narrow opaque zones and wider hyaline zones. The opaque bands were distinct around the entire surface of the medioventral arm of the section and were counted as annuli. Otolith annuli also were most difficult to separate at older ages.

To test the hypothesis that observed rings were formed only once annually, we calculated mean monthly marginal growth on scales by month of collection for all aged fish. Minimum values were unimodal for all age classes; fish from the Atlantic areas showed annulus formation during April and May, whereas Gulf of Mexico fish formed annuli during June and July (Fig. 1). Young-of-year fish collected in West Florida had mean lengths of 36.2 mm in July (N = 10; SD = 9.41), 68.2 mm in August (N = 22; SD = 15.4), 82.7 mm in September (N = 34; SD = 16.7), and 103.5 mm in October (N = 11; SD = 28.5). Samples of otoliths were not available for all months, but 18 1-year-old fish collected during June in the Carolinas showed the beginning of new growth just beyond an annulus at the section edge, indicating that scale and otolith annulus formation occurs simultaneously.

Given simultaneous annulus formation, scales and otoliths obtained from the same fish should show the same number of annuli, and mean lengths at each age as determined from scales and otoliths obtained from fish within the same population should agree. For 43 fish, we determined age from scales and otoliths independently. The agreement was 77%. Of the ten disagreements, nine involved a difference of 1 year and one a difference of 2 years. Observed

TABLE 1.—*Mean range and standard error of the mean (SE) of observed total length in mm for red snappers aged by otoliths and scales from the Carolinas 1974–1978.*

	Aged by scales				Aged by otoliths			
Age	*N*	Mean length	Length range	SE	*N*	Mean length	Length range	SE
1	27	224	137–336	13.2	18	188	137–335	12.2
2	14	379	288–427	9.8	16	337	218–401	11.2
3	15	453	391–497	8.7	7	457	395–490	14.3
4	49	536	435–610	5.5	13	536	460–570	8.2
5	75	577	515–718	4.0	10	579	510–630	13.1
6	65	629	520–732	5.5	8	657	612–685	8.4
7	35	684	605–795	7.4	11	721	645–755	8.6
8	12	753	692–815	11.2	7	769	731–805	10.2
9	7	786	720–806	12.0	7	814	800–840	5.3
10	4	845	820–875	13.2	4	844	812–875	15.3
11	14	855	820–910	6.7	4	841	824–850	6.1
12	8	893	860–930	9.4	1	830		
13	2	867	856–878	11.0	3	873	856–885	6.0
14	2	943	930–955	12.5	1	888		
15	1	1,025			2	910	890–930	20.0
16	1	978						

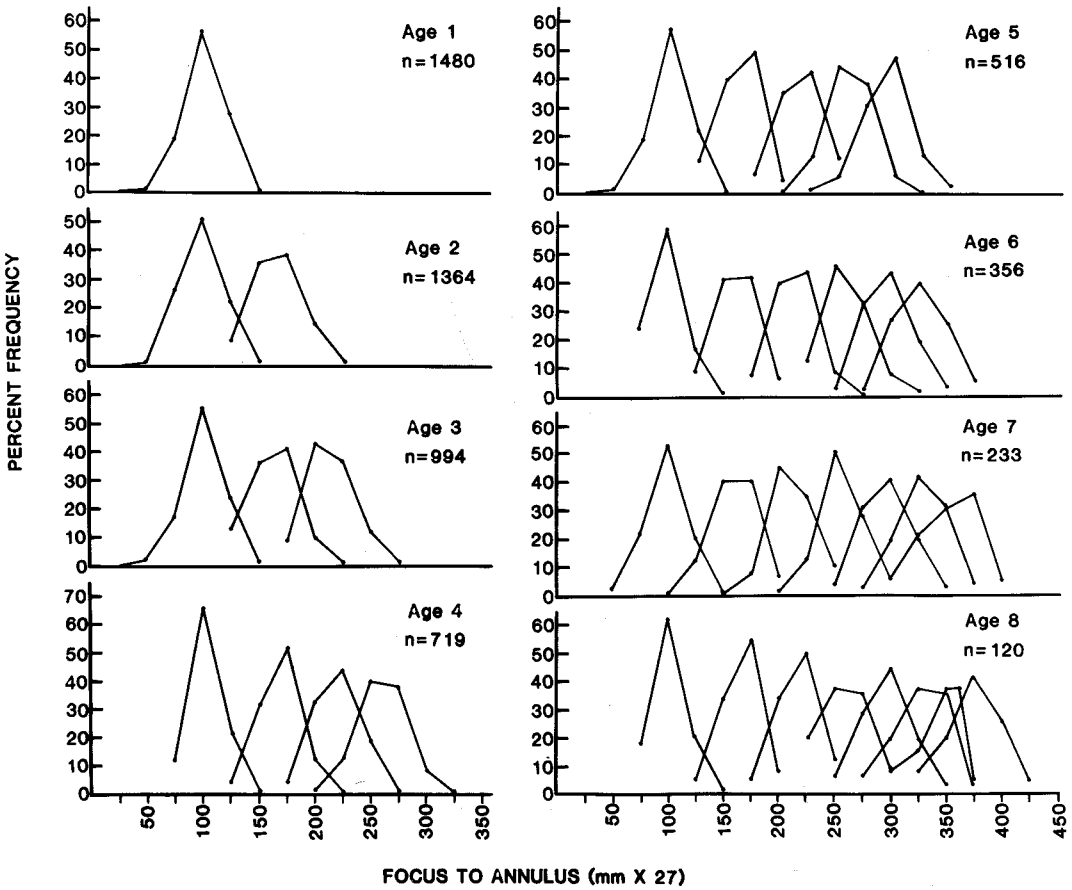

FIGURE 2.—*Frequency distributions of measurements from scale focus to each annulus for red snappers aged 1 to 8 years.*

TABLE 2.—*Weighted back-calculated mean total length (TL) in mm and mean annual increment (MAI) for red snappers by area and age.*

Area		Age 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Louisiana	TL	137	267	379	469	546	613	665	707	751	783	794	891	906			
(scales)	MAI	137	130	112	90	77	67	52	42	44	32	11					
	N	402	382	247	170	131	111	86	53	22	11	4	1	1			
West Florida	TL	177	298	390	470	538	597	642	675	723	762	784					
(scales)	MAI	177	121	92	80	68	59	45	33	48	39						
	N	443	424	301	198	121	92	67	33	15	7	1					
East Florida	TL	146	266	354	448	527	601	652	690	714	733	780	759				
(scales)	MAI	146	120	88	94	79	74	41	38	24	19	47					
	N	357	288	190	110	72	36	29	18	11	7	2	1				
Carolinas	TL	153	275	357	467	542	607	667	723	748	780	803	830	864	913	969	971
(scales)	MAI	153	122	82	110	75	65	60	56	25	32	23	27	34	49	56	
	N	331	304	290	275	226	151	86	51	39	32	28	14	6	4	2	1
(otoliths)	TL	150	266	356	449	525	585	653	715	770	792	821	855	882	904	939	
	MAI	150	116	90	93	76	59	69	62	55	22	29	34	27	49	35	
	N	112	94	78	71	58	48	40	29	22	15	11	7	6	4	2	
All areas	TL	154	278	371	465	540	606	658	703	740	773	800	829	870	913	969	
pooled	MAI	154	124	93	94	85	66	52	45	37	33	27	29	41	43	56	
(scales)	*N*	1,533	1,398	1,028	753	550	390	268	155	87	57	35	16	7	4	2	

lengths of fish aged by scales compared well with observed lengths of fish aged by otoliths for the Carolinas (Table 1). Analysis of variance revealed no significant ($P > 0.65$) main or interactive effects between length at age and the structure used in determining age.

Observed age as determined from scale annuli was associated directly with increasing length of red snapper from all areas. Frequency distributions of the measurements from scale focus to each annulus exhibited single modes for each age, a consistent increase in modal fish length with increasing annulus number, increasing overlap of distributions as annulus number increased, and decreasing length increments between modes as annulus number increased (Fig. 2).

Further support for our age determinations can be taken from two tagging studies. Beaumariage (1969) reports a mean annual growth increment equivalent to 95 mm TL for red snappers 291–490 mm TL tagged and recaptured on the west coast of Florida. Our data (Table 2) indicate mean annual increments of 98 mm TL for fish in the same size range. Moe (1969) mentions the return of a red snapper 5.8 years after it was tagged at 370 mm TL near St. Augustine, Florida. The monthly growth increment between captures was 6 mm TL. Our data from East Florida indicate mean monthly growth increments of 5.2 mm TL for fish between 3 and 9 years of age.

We feel the data support our hypothesis that observed rings are annual marks. Both scales and otoliths are useful for estimating age, but scales are easier to collect and process. The use of both scale and otoliths is advised when sample sizes are small, and for fish greater than 800 mm TL.

Growth

We determined growth rates from observed lengths and back-calculated lengths. Because fish from the Gulf and fish from the Atlantic were not sampled equally over the same time span, observed length is not a reliable indicator of growth differences. Therefore, we compared only back-calculated lengths.

In order to back-calculate lengths, we first determined the relation between fish length and scale radius. This was best described by the regression of $\log_{10}$ scale radius on $\log_{10}$ fish TL. Analysis of covariance revealed no significant effect associated with sex, but a highly significant ($P < 0.001$) effect associated with area of collection. The equations describing the fish-length : scale-radius relation for each area were

TABLE 3.—*Growth parameters and asymptotic standard errors (ASE) calculated from the von Bertalanffy growth equations* ($L_t = L_\infty(1 - e^{-K(t-t_0)})$) *for red snappers, 1974–1979, by area.* L_∞ *is the average length at the asymptotic age predicted by the equation,* K *is the growth coefficient, and* t_0 *is the hypothetical age at which fish would have zero length if they had always grown in the manner described by the equation.*

Parameter	Louisiana	West Florida	East Florida	Carolinas	Gulf of Mexico, pooled	Atlantic Ocean, pooled	All areas, pooled
L_∞	950	941	970	970	941	975	970
ASE	13.5	16.1	19.9	10.5	11.0	9.3	8.0
K	0.175	0.170	0.155	0.165	0.170	0.160	0.162
ASE	0.005	0.005	0.006	0.004	0.004	0.003	0.002
t_0	0.10	−0.10	−0.01	−0.01	−0.10	0.00	0.010
ASE	0.021	0.025	0.025	0.024	0.018	0.017	0.012

Louisiana

$$\log_{10} TL = 1.109 \log_{10} SCL + 0.014; \quad N = 403; \quad r^2 = 0.98;$$

Panama City

$$\log_{10} TL = 1.044 \log_{10} SCL + 1.787; \quad N = 513; \quad r^2 = 0.98;$$

Daytona

$$\log_{10} TL = 1.074 \log_{10} SCL + 0.092; \quad N = 356; \quad r^2 = 0.96;$$

Carolinas

$$\log_{10} TL = 1.067 \log_{10} SCL + 0.117; \quad N = 332; \quad r^2 = 0.96;$$

SCL = magnified scale radius (mm × 27). For each fish, all annuli measurements were substituted for *SCL* in the appropriate equation. The weighted mean TL at the time of annulus formation and weighted mean annual growth increment for each age group then were calculated (Table 3).

The mean back-calculated lengths are close to those presented by Moseley (1966) for Texas and Futch and Bruger (1976) for Florida. Moseley showed annual growth increments of approximately 90 mm standard length from the end of the first year through the end of the fourth year. Futch and Bruger reported weighted mean lengths of 151, 316, 401, 473, and 554 mm TL (converted from FL to TL) for ages 1 through 5 caught off Clearwater, Florida. In our study, first-year growth was highest for West Florida (177 mm), followed by that for the Carolinas (153 mm), East Florida (146 mm), and Louisiana (137 mm). There did not appear to be any predictable pattern of increase or decrease of mean length at the early ages (Lea's phenomenon) (Tesch 1968; Nelson 1980).

The von Bertalanffy growth equation has received much attention regarding the appropriateness of its application (Knight 1968; Yamaguchi 1975; Bayley 1977). In this study, the plot of observed length on age as well as the length-frequency distributions of annuli suggested asymptotic growth. No pronounced inflection was present in the curve over the younger age groups, and samples included representatives of age groups 1–16 collected throughout the year. Therefore, we chose the von Bertalanffy model as an empirically based description of growth. The equation is

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) + E_t;$$

where L_t is length at age t (years), K is the growth coefficient, L_∞ is the average length at the asymptotic age predicted by the equation, t_0 is the hypothetical age at which fish would have zero length if the fish had always grown in the manner described by the equation, and E_t is the error associated with age determination.

Procedure NLIN, which uses the Marquardt method as contained in the Statistical Analysis System package (Helwig and Council 1979), was used to fit length at time of each annulus formation to the growth equation. The procedure utilizes weighted least-squares estimates of the parameters of nonlinear models, calculates residuals, and regresses residuals on the partial derivatives of the model until the iterations converge. All estimates for L_∞ are consistent with maximum observed lengths in each area (Table 3).

The effect of area of collection on the fit of the growth equations was evaluated with a modification of the maximum-likelihood-ratio test (Neeter and Wasserman 1974; Nelson 1980). The von Bertalanffy equation was fit to the data by area, and the residual sums of

squares and degrees of freedom were totalled to give a full-model residual sum of squares, $RSS(F)$ and degrees of freedom, $\mathrm{df}(F)$. The von Bertalanffy equation was then fit to all data combined to obtain a reduced-model residual sum of squares, $RSS(R)$ with corresponding degrees of freedom, $\mathrm{df}(R)$. An F-statistic was calculated by the equation:

$$F = \frac{RSS(R) - RSS(F)}{\mathrm{df}(R) - \mathrm{df}(F)} \div \frac{RSS(F)}{\mathrm{df}(F)}.$$

The effect of area was significant ($P < 0.01$) for all study areas, for pooled Atlantic data compared to pooled Gulf data, for areas within the Gulf, and for areas within the Atlantic. Although significant statistically, the actual differences are small. Data for populations within the Gulf and within the Atlantic are certainly similar enough to be pooled. Thus, red snappers of ages 1 through 5 from the Atlantic would have predicted lengths of 144, 264, 369, 458, and 533 mm at the time of annulus formation, and those from the Gulf 160, 283, 385, 472, and 546 mm. By the time a fish from the Gulf was 10 years of age it would reach 772 mm and a similarly aged fish from the Atlantic would be 778 mm.

Analysis of covariance indicated that the relationship between length and weight differed between areas ($P < 0.01$), but not between sexes ($P > 0.50$). Although statistically significant, the biological implications of area differences seem minimal. On the average, a 500-mm fish would weigh 1,842 g if taken off West Florida, 1,889 g if taken off East Florida, and 1,951 g if caught off the Carolinas. The equations are

West Florida $W = 1.82 \times 10^{-5}\, TL^{2.966}$; $N = 143$; $r^2 = 0.99$;

East Florida $W = 1.36 \times 10^{-5}\, TL^{3.017}$; $N = 142$; $r^2 = 0.99$;

Carolinas $W = 3.15 \times 10^{-5}\, TL^{2.887}$; $N = 177$; $r^2 = 0.99$;

All areas, pooled $W = 2.04 \times 10^{-5}\, TL^{2.953}$; $N = 462$; $r^2 = 0.99$;

W is weight in grams.

The data do not allow an assessment of variation in growth between individual reef systems. Overall geographic patterns are probably the result of differing rates of growth on many distinct reef systems.

Mortality Estimates

Age–length keys derived from aged fish were applied to all fish collected, and catch curves then were constructed (Fig. 3). Fish used in age determinations were selected randomly from the total catch, and keys were constructed separately for each area, so this method should not bias the resulting estimates of total mortality (Westrheim and Ricker 1978).

Analysis of covariance showed no effect due to year on the slope of the regressions from East Florida and the Carolinas, and the regression of Z on year of collection showed no trend of increase or decrease in mortality over the years sampled, so years were pooled to yield the best estimate (Table 4). Area did have an effect on the mortality regressions ($P < 0.01$). Louisiana showed the highest rate of instantaneous total mortality (0.78 by regression; 0.94 by Robson and Chapman 1961), East Florida an intermediate rate (0.50; 0.50), and West Florida (0.42; 0.44) and the Carolinas (0.39; 0.42) the lowest rates. The mean age in the catch was 2.4 years for Louisiana, 4.1 years for West Florida, 3.0 years for East Florida, and 6.1 years for the Carolinas. There was a strong negative correlation ($r = -0.83$) between instantaneous mortality and mean age.

Studies of other fish species in the deep-reef taxocene (red porgy *Pagrus pagrus*; vermilion snapper *Rhomboplites aurorubens*) have demonstrated depth-specific size segregation (Manooch and Huntsman 1977; Grimes 1978). The fishing grounds off the Carolinas can be divided into inshore (<35 m depth) and offshore (>35 m depth) habitats. To evaluate the size distribution of red snapper we compared length distributions, catch curves, and estimated mortality (Z) for fish collected inshore and offshore. Length distributions were similar. The modal length classes were 575–600 mm inshore and 600–625 mm offshore. Both groups of data showed a modal age of 6 years, and analysis of covariance revealed no difference in mortality between inshore ($Z = 0.42$) and offshore ($Z = 0.38$) data. Few red snappers were taken inshore, and most of these were from the deepest inshore reefs. No size segregation by depth is evident.

The Pauly (1980) method of determining M depends on the mean annual temperature (T), and parameters of the von Bertalanffy equation as follows: $\log_{10} M = 0.654 \log_{10} K - 0.280$

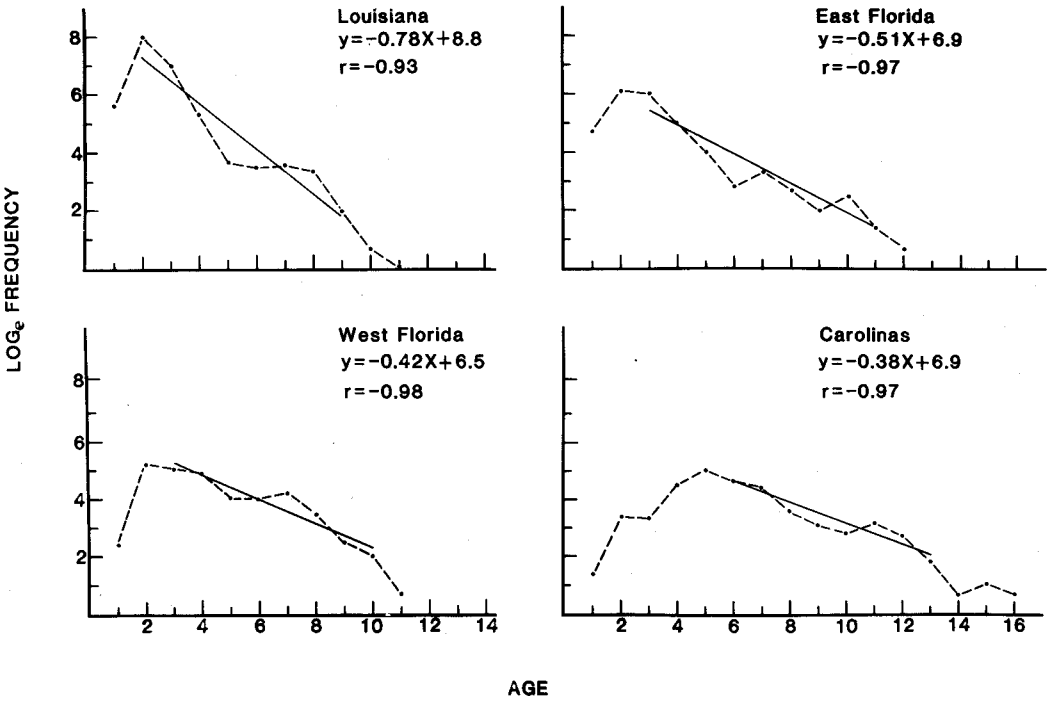

FIGURE 3.—*Catch curves for red snappers from all areas. The solid line described by the equation* (y = bx + a; y = log_e *frequency;* x = *age in years) indicates the age range used in regression estimates of total annual instantaneous mortality* (Z). Z *is equal to the absolute value of the slope* (b) *of the regression line.*

$\log_{10} L_\infty + 0.463 \log_{10} T$. In calculating M, we used 50-year mean temperatures with 75 m as a standard depth. The mean annual temperature was 22 C for Louisiana, 22 C for West Florida, 24 C for East Florida, and 21 C for the Carolinas (Churgin and Halminski 1974a, 1974b). All estimates of M are virtually the same. Inasmuch as there is little or no variation in the abiotic regime and predator and prey species assemblages among deep-reef habitats throughout the range of our study, we would expect to find little difference in natural mortality. A possible shortcoming of the Pauly method is that there is no way to include information about the age–size structure of the population in the calculation of M.

Both methods used to calculate Z are subject to the assumptions that: (1) recruitment and survival are constant in the population under examination; (2) fishing effort has been constant over the time span represented by the oldest fish in the age series examined; (3) the sample is random; and (4) for the population in question all size classes should be present within the area of collection. To address the first assumption we examined a series of length-fre-

TABLE 4.—*Modal and mean age of the catch in years, and instantaneous rates of total* (Z), *natural* (M), *and fishing* (F) *mortality for all areas.* M *was determined by the method of Pauly (1980),* Z *by catch-curve regression and by the method of Robson and Chapman (1961), and* F *by difference.*

				Regression		Robson and Chapman	
Area	Modal age	Mean age	M	Z (SE)	F	Z (SE)	F
Louisiana	2	2.4	0.20	0.78 (0.11)	0.58	0.94 (0.04)	0.74
West Florida	2–3	4.1	0.19	0.42 (0.05)	0.23	0.44 (0.09)	0.25
East Florida	2–3	3.0	0.19	0.50 (0.07)	0.31	0.50 (0.04)	0.31
Carolinas	5	6.1	0.18	0.39 (0.05)	0.21	0.42 (0.04)	0.24

quency histograms and catch curves for the Carolinas (1974–1978) and East Florida (1976–1978). In all cases, modal age was constant by area over the years examined, the mean age in the catch did not differ over the years within area, and there were no unusually weak or strong year classes apparent during the period examined. As previously mentioned, Z did not vary between years in these areas. We feel that the first assumption probably is satisfied, and that any variation in survival or recruitment within the age series examined is random. Mortality estimates derived by the regression method are least sensitive to minor violations of this assumption (Ricker 1975; Robson and Spangler 1978), and all statistical tests are performed on these estimates. Fishing effort, as indicated by the number of active vessels, did not change appreciably during the course of this study in the Carolinas, East Florida, or West Florida. We do not think effort in the Gulf commercial fishery has changed significantly. Whether hook-and-line fishing is a random method of collection is not clear. It certainly excludes fish not actively feeding. Although hook sizes used do exclude smaller fish, they do not seem to affect size frequencies in the range used for mortality estimates. We think our sample is a true random sample of the catch, and that the catch is representative of red snapper populations within the age series examined in each area.

Fishing mortality appears to be the major cause of differences among total mortality rates. Catches for the intensive commercial fishery off Louisiana and for the recreational fishery off East Florida, where the reefs are fairly close to shore and easily accessible, are similar in age structure and reflect the highest mortality rates. The recreational fisheries off West Florida and the Carolinas are located farther offshore and require larger boats and more sophisticated electronic gear to be exploited successfully. Both of these areas exhibit lower mortality rates than the other areas and catches are composed of older, larger fish. Fisheries in the Gulf and East Florida have much longer histories than the one off the Carolinas (Camber 1955; Huntsman 1976). The age structure of red snapper off the Carolinas reflects the relatively light fishing pressure and short history of the fishery. A large fraction of the total biomass consists of large, older individuals, a condition indicative of systems subject to little exploitation (Regier et al. 1979). Manooch and Huntsman (1977), discussing a similar situation regarding red porgy from off the coasts of North Carolina and South Carolina, concluded that mortality was largely the result of natural causes and that fishing played only a minor role.

Conclusions

The red snapper, although resident in a functionally tropical habitat (Huntsman and MacIntyre 1971; Smith et al. 1975), can be aged by annular markings on both scales and otoliths. We found that annulus formation occurs in April and May in the Atlantic and June and July in the Gulf of Mexico. The formation of annuli does not seem to be associated with winter temperature minima. Camber (1955) thought that red snappers ceased feeding during the spawning season, and Moseley (1966) believed a feeding cessation during spawning periods accounted for annulus formation. Although our data support this hypothesis, the presence of an annulus on age-1 (immature) fish could indicate that some innate physiological rhythmn, correlated with external factors that control spawning, might be the stimulus for annulus formation. Hickling (1935) suggested this explanation in connection with annulus formation in juvenile hake *Merluccius merluccius*. Red snappers become sexually mature after 2–3 years (Bradley and Bryan 1975).

In general, growth of the red snapper and other species common to the outer reef habitats is similar. The K values of the growth equation for red snapper ranged from 0.155 to 0.175. Other workers have shown similar K values for the vermilion snapper (0.198: Grimes 1978), the yellowtail snapper *Ocyurus chrysurus* (0.160: Piedra 1969), the red grouper *Epinephelus morio* (0.179: Moe 1969), the red hind *Epinephelus guttatus* (0.180: Burnett-Herkes 1975), and the white grunt *Haemulon plumieri* (0.1084: Manooch 1978). Growth for these species is initially fast and then slows steadily, as larger sizes associated with long life expectancy are attained. Although most predatory pelagic fishes from these same general areas do not live as long as species in the reef-fish complex, growth is fast throughout their lives, with K values of from 0.23 to 0.34 for bluefish *Pomatomus saltatrix* and 0.48 for Spanish mackerel *Scomberomorus maculatus* (Huntsman and Manooch 1978). In Brazil, the Caribbean red snapper appears

to reach the same size as the red snapper, but grows more slowly, with a coefficient (K) of 0.090 (de Menezes and Gesteira 1974).

The total annual mortality and age structure of the catch seems to reflect the amount of fishing pressure in each study area. The fishing component of mortality appears to account for the variation in Z between all areas.

Significant differences in mortality and age structure of the populations of red snapper in the four areas would have more impact on management models than the slight, but significant differences in growth. Similar differences may also exist for other species in the deep-reef taxocene.

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