Age and growth of the yellowedge grouper, *Epinephelus flavolimbatus*, and the yellowmouth grouper, *Mycteroperca interstitialis*, off Trinidad and Tobago

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Abstract.—Age and growth were determined for the yellowedge grouper, *Epinephelus flavolimbatus,* and the yellowmouth grouper, *Mycteroperca interstitialis,* off Trinidad and Tobago. Age was determined from cross sections of sagittae and opaque rings were counted as annuli. From the monthly variation in marginal increment ratio (marginal increment divided by the distance between the penultimate and outermost annulus), rings were found to be deposited annually from October to February in the yellowedge grouper. Monthly variation in the frequency of otoliths with an opaque margin showed that opaque rings were deposited from September to January in the yellowmouth grouper. Both species were found to grow slowly, to have long lifespans, and to achieve high asymptotic lengths. Ages between 3 and 35 years (282–985 mm TL) were found for the yellowedge grouper, for which the von Bertalanffy growth equation was $L_t = 963 (1–e^{–0.099(t+0.08)})$, where L_t is length (mm) at time t (yr). Yellowmouth groupers between ages 5 and 41 years (335–827 mm FL) were found and the von Bertalanffy growth equation was $L_t = 854 (1–e^{–0.057(t+4.6)})$. The length-weight relationship for the yellowedge grouper was $Wt = 5 \times 10^{–5}TL^{2.80}$, where Wt is body weight (g) and TL is total length (mm). For the yellowmouth grouper this relationship was $Wt = 1.88 \times 10^{–5}FL^{2.94}$, where FL is fork length (mm). Both species appear to grow more slowly and to achieve a greater asymptotic size and age than populations in higher latitudes, in contrast to what was expected based on differences in environmental temperature. This may be attributed to differences in fishing pressure because the populations in this study might have been subjected to a lower level of exploitation over a shorter period of time.

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The yellowedge grouper (*Epinephelus flavolimbatus*) and the yellowmouth grouper (*Mycteroperca interstitialis*) are two large serranids commonly caught in the trap fishery off Trinidad and Tobago. The yellowedge grouper has been recorded from North and South Carolina (Huntsman, 1976), the Gulf of Mexico, the West Indies, and the north coast of South America to Brazil at depths of 35–370 m (Smith, 1978). The yellowmouth grouper is found in rocky areas from the shoreline to depths of at least 55 m and is distributed from Bermuda, the South Atlantic Bight, the Gulf of Mexico, throughout the West Indies, Venezuela and Brazil (Smith, 1978), replacing the northern species *M. phenax* in some areas.

Both species are of significant commercial value in Venezuela (Smith, 1971; Gonzalez and Celaya[1]). The yellowmouth grouper is also commercially exploited in Bermuda (Smith, 1971) and the eastern Gulf of Mexico (Bullock and Murphy, 1994). Groupers are also of commercial importance in Trinidad and Tobago where they form part of a lucrative export trade in chilled fish. Yellowedge and yellowmouth groupers are the most commonly caught groupers in traps and are also caught by handlines (Manickchand-Heileman and Phillip, 1993). Historically, these species have been fished on the continental shelf and shelf edge northwest of Tobago and along the north and northeastern coasts of Trinidad by artisanal vessels from Trinidad and Tobago, as well as from Venezuela (Mendoza and Larez, 1996). Due to the decline in catch rates in these areas (Manickchand-Heileman and Phillip, 1993; Mendoza and Larez, 1996), the fishery has expanded to

[1] Gonzalez, L.W., and J. Celaya. 1986. Diagnostico socio-economico de la pesqueria de media altura pargo-mero del estado Nueva Esparta. Contrib. 8, Centro de Investigaciones Cientificas, Univ. Oriente, Venezuela. 31 p. Univ. del Oriente, Apdo. Postal 245, Cumana, Sucre, Venezuela.

the offshore continental shelf and shelf edge to the east of Trinidad. At present, this fishery is not managed and the decline in catches in the traditional fishing areas emphasizes the need for proper management. However, lack of data is an impediment to the development of appropriate management strategies for this important fishery.

Groupers are relatively long-lived and slow-growing and are protogynous hermaphrodites, making them especially susceptible to overexploitation (Bannerot et al., 1987; Shapiro, 1987; Bohnsack[2]). In reviewing the status of grouper stocks in the western central Atlantic, Sadovy (1990) found that these stocks are heavily fished throughout the region and that many are growth or recruitment overfished, or both. Sadovy also emphasized the need for management to ensure their continued commercial and recreational viability.

Published information on the yellowedge and yellowmouth grouper is scarce. Age, growth and reproduction of the yellowedge grouper in South Carolina have been investigated by Keener (1984) and in the eastern Gulf of Mexico by Bullock and Godcharles.[3] Randall (1967) documented the food habits of yellowmouth grouper from the Bahamas and Thompson and Munro (1978) recorded the occurrence of spawning individuals in Jamaica. Aspects of the life history, including age and growth, of yellowmouth grouper in the eastern Gulf of Mexico have been reported by Bullock and Smith (1991) and Bullock and Murphy (1994).

In Trinidad and Tobago, information on reproduction, age, and growth of the yellowedge and yellowmouth groupers have been presented by Manickchand-Heileman and Phillip.[4] However, age was not validated and results were only preliminary. Our study reports on the age and growth of these two species off Trinidad and Tobago. It was carried out as part of a national fish stock assessment project, in collaboration with the Fisheries Division, Ministry of Agriculture, Lands and Marine Resources (Trinidad and Tobago), the United Nations Development Program (UNDP), and the Food and Agriculture Organization (FAO).

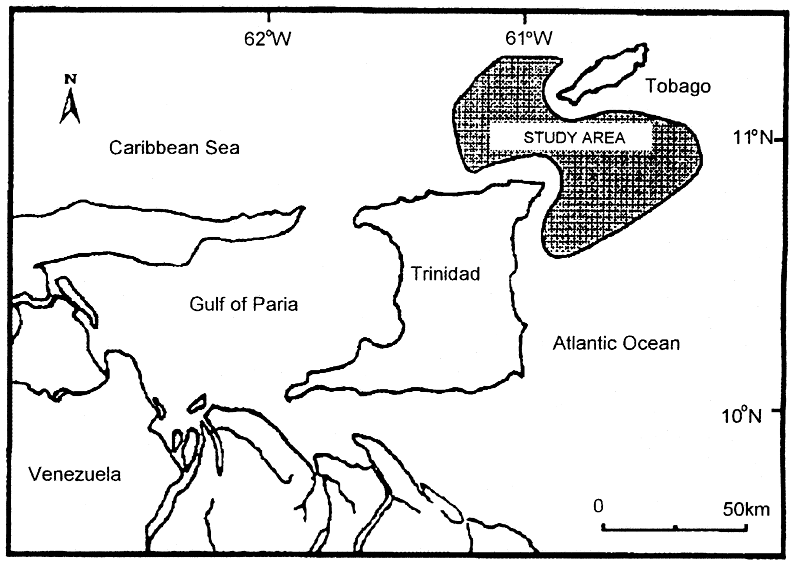

Figure 1
Location of study area.

Materials and methods

Study area

Trinidad and Tobago, a twin-island Republic, are the southernmost of the Caribbean chain of islands (Fig. 1). Both islands are situated on the South American continental shelf; Tobago is about 32 km to the northeast of Trinidad. Topographically, the shelf in this area is relatively featureless; a substratum of fine mud is interspersed with occasional patches of shell debris and fine sand (Kenny and Bacon, 1981). The shelf edge lies along the 90–100 m contour (Gade[5]) which ranges from a distance of approximately 12 km from the northwest coast of Tobago to approximately 50 km from the north coast of Trinidad.

This area experiences a dry season from December to May and a wet season from June to November. Bottom temperatures at depths of about 100 m vary from a maximum of 25°C in the dry season to a minimum of 22°C in the wet season (Gade[5]). During the wet season the large input of fresh water from

[2] Bohnsack, J. A. 1989. Protection of grouper spawning aggregations. Coastal Resour. Div. Contrib. Rep. CRD 88-89-06, NMFS Southeast Fish. Sci. Cent., Miami, FL, 8 p.

[3] Bullock, L. H., and M. F. Godcharles. 1984. Life history aspects of the yellowedge grouper, *Epinephelus flavolimbatus* (Pisces: Serranidae) from the eastern Gulf of Mexico. Annual Report, Fla. Dep. Nat. Resour., Mar. Res. Lab., St. Petersburg, FL, 28 p. Unpubl. data.

[4] Manickhand-Heileman, S., and D. A. T. Phillip. 1992. Preliminary stock assessment of the fishpot fishery of Tobago. Technical report of the Project for the Establishment of Data Collection Systems and Assessment of the Fisheries Resources. Report FAO/UNDP:TRI/91/001/TR12, 38 p.

[5] Gade, H. 1989. The environmental-ecological regimes. *In* Report on surveys of the fish resources in the shelf areas between Suriname and Colombia with the R/V *Dr. Fridtjof Nansen*, p. 8–41. Institute of Marine Research, Bergen.

local precipitation and runoff from South American rivers, particularly the Orinoco River, affect surface salinity which ranges from 35.5‰ in the dry season to less than 27‰ in the wet season. However, the salinity of deeper waters is not greatly affected and ranges from about 36.8‰ in the wet season to 36.5‰ in the dry season (Gade[5]).

Methods

Monthly samples of yellowedge and yellowmouth grouper were obtained from commercial fish landings at a fish processing plant on the island of Tobago. Fish were caught by Antillean fish traps (Munro et al., 1971) on the continental shelf and slope to the northeast of Trinidad and northwest of Tobago in depths of 37–128 m (Fig. 1). A total of 729 yellowedge and 116 yellowmouth groupers were obtained during the study period.

Total length (mm) was recorded for the yellowedge grouper, whereas fork length (FL) was recorded for the yellowmouth grouper because, in most cases, the filamentous rays of the caudal fin of this species were damaged. Total body weight (g) was recorded for both species. For most fish the left sagittal otolith was removed unless broken or lost, in which case the right was obtained. Otoliths were stored dry in labelled envelopes.

For sectioning, otoliths were embedded in Spurr resin (Spurr, 1969) and allowed to harden overnight. One or two 0.5-mm transverse sections of each otolith were taken through the focus along a dorsoventral plane with a high-speed circular saw. Sections were ground and polished with several grades of silicon carbide paper. They were placed in glycerol and viewed against a black background with reflected light under a dissecting microscope at a magnification of 20×. Alternating opaque and translucent bands were visible and the former were counted as annuli.

For each species, otolith radius (distance from the core to the otolith edge) and the distance from the core to the distal edge of each opaque ring were measured under a binocular microscope with an ocular micrometer (1 micrometer unit=0.125 mm). All measurements were taken along the ventral surface of the sulcus acousticus. In order to validate that rings were formed annually in the yellowedge grouper, the monthly mean marginal increment ratio, that is, the marginal increment (distance between the distal edge of the outermost annulus and the otolith margin) divided by the distance between the distal edge of the penultimate annulus and proximal edge of the outermost annulus (Bullock et al., 1992), was calculated. Because of difficulty in measuring annulus radius in the yellowmouth grouper, it was not possible to carry out this analysis in sufficiently large monthly samples. Instead, for this species the monthly frequency of occurrence of otoliths with an opaque edge was determined. Mean monthly marginal increment ratios in the yellowedge grouper and frequency of occurrence of opaque edges in the yellowmouth grouper were compared by using the chi-square goodness-of-fit test for circular data (Zar, 1974). Least squares linear regression of otolith radius on fish length was carried out and the relationship used to backcalculate lengths of fish at earlier ages.

The von Bertalanffy growth function was used to describe growth (Ricker, 1975):

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right),$$

where L_t = total or fork length (mm) at time t (years);
L_∞ = the asymptotic length;
K = the growth coefficient; and
t_0 = theoretical age at zero length.

This function was fitted to observed lengths at age by using the FISHPARM program (Prager et al., 1987). The length-weight relationship was determined by least squares linear regression with logarithmically transformed data:

$$W = aL^b,$$

where W = body weight (g);
L = fish length (mm); and
a and b are constants.

Results

Validation

Satisfactory annuli counts were made on 326 of the 367 yellowedge grouper otoliths examined. A randomly chosen subsample of 63 otoliths was read by an independent reader and a 95% agreement was found. This species showed a significant difference among monthly mean marginal increment ratios (P<0.001), with elevated values (greater than 50%) occurring from March to September (Fig. 2). This finding suggests that there is one main period of annulus formation during the year from October to February, even though otoliths with opaque edges were observed throughout the year.

Growth of the otolith was proportional to growth in length of the fish and the relationship between total length (TL) and otolith radius (OR) was

$$TL = 111.4OR - 105.2 \quad (n=330,\ r^2=0.93).$$

Number of rings increased with fish length; 3–35 rings were found in yellowedge grouper between 282 and 985 mm TL.

Of the 90 otoliths read for the yellowmouth grouper, satisfactory annuli counts were made on 80. A random subsample of 33 otoliths was read by an independent reader and a 98% agreement was found. For this species frequency of otoliths with an opaque edge showed significant monthly variation ($P<0.001$), with elevated values occurring from September to January (Fig. 3). Growth of the otolith was proportional to growth in length and the relationship between fork length (FL) and otolith radius was

$$FL = 162.97 + 90.86OR \quad (n=57,\ r^2=0.81).$$

The number of rings increased with fish length; 5–41 rings were found in yellowmouth grouper between 335 and 827 mm FL.

The monthly sample sizes shown in Figures 2 and 3 indicate the seasonal pattern of catches for both species in this study area. At the extremities of the year, catches were low because fishing is restricted to shallow waters owing to rough seas that prevail at this time.

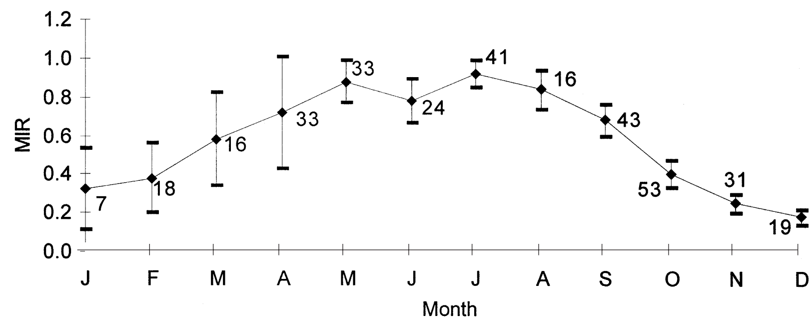

Figure 2

Monthly variation in mean marginal increment ratio (MIR) for yellowedge grouper, *E. flavolimbatus*. Sample sizes are given next to means and standard deviation is represented by the horizontal bars .

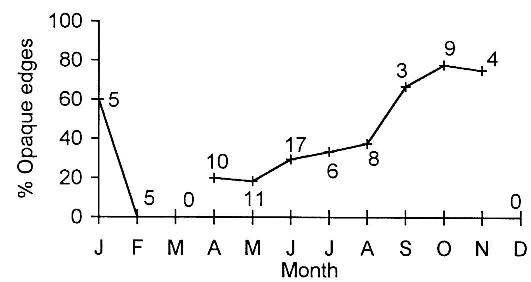

Figure 3

Monthly variation in the frequency of occurrence of otoliths with opaque margin for yellowmouth grouper, *M. interstitialis*. Sample sizes are given next to data points.

Age and growth

For both species, the growth parameters are presented for combined sexes because in some instances otoliths were obtained from fish that were gutted at sea and thus of unknown sex. The relationship between fish length and otolith radius was used to backcalculate lengths of fish at earlier ages. Owing to the narrowing of the space between successive annuli in older individuals and the resulting difficulty in making accurate measurements, radii were measured in 231 yellowedge grouper with 3 to 15 rings. Mean backcalculated lengths for yellowedge grouper are given in Table 1. Close agreement was found between the observed, backcalculated, and theoretical growth curves for this species, although for some age groups the backcalculated lengths were greater than observed lengths (Fig. 4). The von Bertalanffy growth parameters (asymptotic standard error) for observed length and age data for the yellowedge grouper were L_∞ = 963 mm TL (18.8 mm), K= 0.099/yr (0.01 yr), t_0= –0.08 years (0.28 yr).

Owing to narrowing of the space between annuli in older individuals and difficulty in making accurate measurements, it was possible to measure radii in only 20 yellowmouth grouper, with 5 to 19 rings. Mean backcalculated lengths for yellowmouth grouper are given in Table 2. Close agreement was also found between the observed, backcalculated and theoretical growth curves for this species, although some backcalculated lengths were greater than observed lengths, particularly for the younger age groups (Fig. 5). For the yellowmouth grouper, the von Bertalanffy growth parameters (asymptotic standard error) for observed length at age data were L_∞ = 854 mm FL (59.9 mm), K= 0.057/yr (0.01/yr), t_0= –4.6 years (2.29 yr).

Length-weight relationship

For the yellowedge grouper, the relationship between total body weight (Wt) and length (TL) was

Table 1

Observed and backcalculated mean total lengths (TL mm) at age (yr) for the yellowedge grouper, *E. flavolimbatus*. Roman numerals represent annulus number, beginning at the focus of the otolith.

Age (yr)	*n*	Mean TL (mm)	SD (mm)	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
3	3	317	14	185	251	313												
4	2	299	23	123	198	241	294											
5	15	389	24	136	203	269	331	381										
6	29	438	35	128	206	277	340	395	431									
7	41	469	47	120	194	265	334	389	434	465								
8	33	534	50	126	209	281	350	412	461	502	530							
9	26	586	61	135	221	300	363	426	478	519	552	579						
10	22	618	44	135	220	292	360	420	469	513	552	578	605					
11	32	638	36	124	202	281	353	411	466	511	550	583	612	629				
12	13	666	74	129	197	259	333	400	451	497	537	577	610	638	659			
13	6	696	61	162	215	290	354	408	452	492	534	573	610	644	669	690		
14	5	725	72	129	197	250	317	369	423	474	517	545	586	623	661	694	718	
15	4	769	57	121	201	264	327	382	442	482	519	562	603	640	677	709	743	766
Total	231																	
Weighted backcalculated mean TL (mm)				129	207	278	345	403	453	497	542	577	607	633	664	696	728	766
Growth increment (mm)					78	71	67	58	50	44	45	35	30	26	31	32	32	38

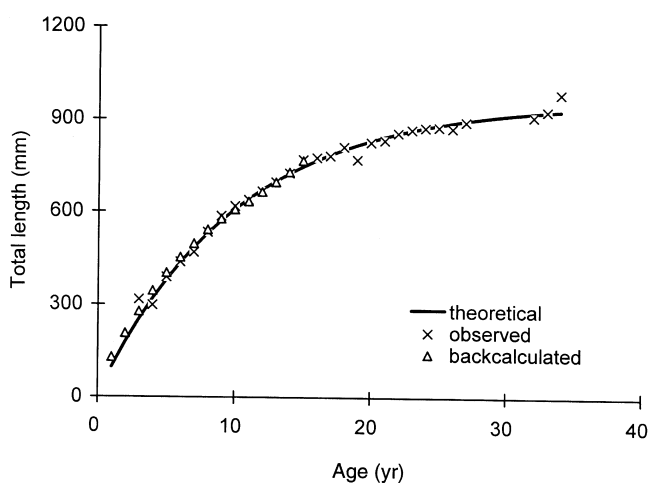

Figure 4

Observed, backcalculated, and theoretical lengths at age for yellowedge grouper, *E. flavolimbatus*.

$$Wt = 5.0 \times 10^{-5} \mathrm{TL}^{2.80} \qquad (n=335,\ r^2=0.88).$$

The exponent b was significantly different from 3 (t-test, t=17.98, P<0.001). For the yellowmouth grouper this relationship was

$$Wt = 1.88 \times 10^{-5} FL^{2.94} \qquad (n=50,\ r^2=0.94),$$

with b being significantly different from 3 (t-test, t=5.19, P<0.001).

Discussion

The annual formation of opaque rings was demonstrated in both yellowedge and yellowmouth groupers in the study area. Deposition of annuli occurs over a protracted period of about five months, beginning in the wet season and continuing into the early part of the dry season. A protracted period of annulus deposition has been observed in other grouper populations, e.g. *Mycteroperca phenax* (Matheson et al., 1986), *Epinephelus itajara* (Bullock et al., 1992), and *M. microlepis* (Hood and Schlieder, 1992). Factors affecting annulus formation in groupers have been discussed by Moe (1969), who attributed annulus formation in red grouper to spawning and related physiological processes. In contrast, in our study area, annulus formation in the yellowmouth and yellowedge groupers occurred after the period of peak spawning from about April to July for both species (Manickchand-Heileman and Phillip[4]). Formation of annuli after spawning was also reported for the Nassau grouper, *E. striatus*, in the Cayman Islands (Bush et al., 1996). Annulus formation has also been found to occur out of phase with spawning in other grou-

Table 2

Observed and backcalculated mean fork lengths (FL mm) at age (yr) for the yellowmouth grouper, *M. interstitialis*. Roman numerals represent annulus number.

Age (yr)	*n*	Mean TL (mm)	SD (mm)	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX
5	3	335	3	234	273	298	320	332														
6	1	355	—	236	262	302	322	335	349													
8	2	482	23	269	315	355	380	411	436	456	474											
9	1	516	—	271	310	349	379	398	428	457	487	506										
10	1	557	—	290	337	372	406	430	453	476	511	534	557									
12	3	566	48	279	321	360	394	418	445	469	492	511	525	544	558							
13	1	603	—	273	346	395	432	456	481	505	530	554	566	579	591	603						
14	5	605	38	277	324	359	382	404	427	449	469	489	508	528	544	555	564					
15	1	559	—	331	321	341	371	391	410	430	450	480	499	519	529	539	549	559				
17	1	634	—	289	335	381	404	427	450	473	496	508	531	554	565	577	588	600	611	623		
19	1	700	—	336	380	405	431	457	475	492	509	527	544	553	579	605	622	626	631	635	639	644
Total	20																					
Weighted backcalculated mean TL (mm)				274	316	351	378	399	434	462	484	506	524	540	555	566	572	595	621	629	639	644
Growth increment (mm)					42	35	27	22	35	28	22	22	18	16	15	11	6	23	26	8	11	4

pers in higher latitudes, e.g. *M. phenax* in the South Atlantic Bight (Matheson et al., 1986), *E. itajara* (Bullock et al., 1992) and *M. microlepis* (Hood and Schlieder, 1992) in the eastern Gulf of Mexico, and *M. bonaci* in south Florida (Crabtree and Bullock, 1998). For the two species in our study, annulus formation may be associated with changes in environmental factors, notably reduced bottom temperature during the wet season. On the continental shelf, where our study was conducted, bottom temperature has been found to decrease to a minimum of about 22°C in the wet season (Gade[5]).

Annual rings were found in otoliths of yellowedge and yellowmouth groupers in other geographical areas, although time of annulus formation differed, which may be attributed to differences in annulus measurement techniques. For yellowedge grouper in the South Atlantic Bight, annulus formation occurred in March–September and coincided with time of peak spawning (Keener, 1984), whereas in the eastern Gulf of Mexico it occurred from May to November (Bullock and Godcharles[3]). The yellowmouth grouper formed annuli in August–October in the eastern Gulf of Mexico (Bullock and Murphy, 1994).

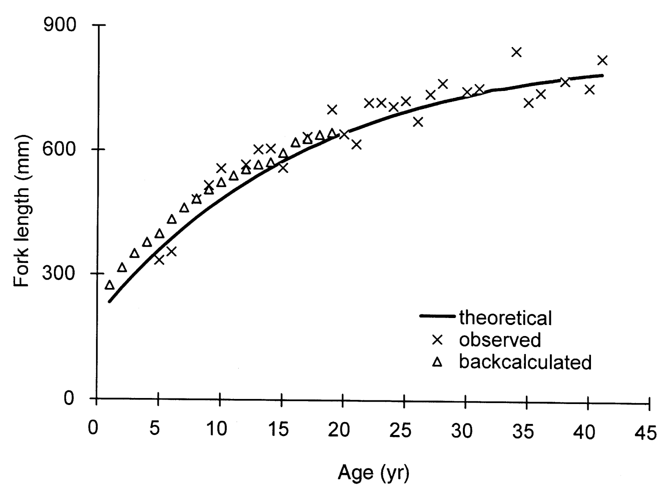

Figure 5

Observed, backcalculated, and theoretical lengths at age for yellowmouth grouper, *M. interstitialis*.

Some backcalculated lengths were larger than observed lengths, especially for the younger age groups. This reverse "Rosa Lee" phenomenon may have resulted from increased survival of fast-growing fish (Ricker, 1975). For the yellowmouth grouper, the small number of fish available for ring measurements may have also contributed to discrepancies in the backcalculated lengths.

The growth pattern of these two species is similar to that reported for other groupers, in that they are long-lived and have low growth rates and high asymptotic lengths (e.g. *M. phenax*, Matheson et al., 1986; *M. bonaci*, Manooch and Mason, 1987, Crabtree and Bullock, 1998; *E. itajara*, Bullock et al., 1992; *M. micro-*

lepis, Hood and Schlieder, 1992; *E. guttatus*, Sadovy et al., 1992). In the southern United States, the yellowedge grouper has a lower asymptotic length and higher growth rate (L_∞=891mm TL, K=0.163, Keener, 1984; L_∞=831 mm TL, K=0.191, Bullock and Godcharles[3]) than those found in our study. Our maximum observed age (35 years) was greater than those (15 and 27 years) reported by Keener (1984) and Bullock and Godcharles,[3] respectively.

Comparison of growth curves using Φ', where $\Phi' = \log K + 2\log L_\infty$ (Munro and Pauly, 1983; Pauly and Munro, 1984) showed close agreement with those in other areas (Φ'=2.96, our study, Φ'=3.11 and 3.12, southern United States with growth parameters of Keener, 1984, and Bullock and Godcharles[3], respectively). This comparison suggests that the general growth pattern of yellowedge grouper observed in our study is similar to that for the southern United States and further validates the results obtained in our study.

The yellowmouth grouper also showed a higher L_∞ (854 mm FL or 934 mm TL) and lower K than reported for the eastern Gulf of Mexico where L_∞ was 828 mm TL and K was 0.076 (Bullock and Murphy, 1994). The maximum observed age (41 years) was higher than that (28 years) reported by Bullock and Murphy (1994). Comparison of growth curves using Φ' showed close agreement between the growth curve obtained in our study (Φ'=2.70) and that obtained by Bullock and Murphy (1994) whose growth parameters resulted in Φ' of 2.72.

Results suggest that the growth curve of each species belongs to the same family of curves as their counterparts in other geographical areas, i.e. the relationship between L_∞ and K is similar (Pauly, 1991). However, comparison of actual growth rates and asymptotic lengths indicates that each species grows slower and achieves a greater size and age than those reported for populations in the southern United States. This finding is in contrast to what is expected in the growth patterns of tropical versus subtropical and temperate populations. Tropical fish generally grow faster and reach smaller sizes than populations in higher latitudes, mainly because of differences in environmental temperature (Longhurst and Pauly, 1987). It appears that factors other than those related to the environment may be responsible for the differences observed, or may mask the real growth pattern. Such factors may include intrinsic differences between populations, or differences in fishing patterns between the two areas. The latter may contribute significantly to differences in growth because grouper populations in the southern United States have been fished since the late 1970s (Bullock and Murphy, 1994; Bullock et al., 1996) for a longer period of time than the populations in our study. Populations subjected to high exploitation rates for long time periods generally exhibit changes in growth and reproductive patterns, such as faster growth and smaller sizes (Gulland, 1983), as well as smaller size at maturity (McGovern et al., 1998) than populations that have not been as heavily fished.

The slow growth, long life spans, and presumed low natural mortality rates of yellowedge and yellowmouth grouper reported for our study, imply that they are highly susceptible to overfishing (Bullock et al., 1992). These characteristics suggest that maximum yield would be obtained at either low exploitation rates or with capture of only large individuals (Bullock et al., 1992). In addition, the protogynous hermaphroditic strategy of some groupers may also make them more susceptible to overfishing than gonochoristic species (Bannerot et al., 1987). Evidence of hermaphroditism has been reported for the yellowedge grouper (Keener, 1984; Bullock et al., 1996) and other species of *Mycteroperca* (Matheson et al., 1986; Collins et al., 1987; Hood and Schlieder, 1992; Crabtree and Bullock, 1998). We did not consider differences in growth patterns and population dynamics specific to an alternative reproductive strategy in our study. For protogynous hermaphrodites, the pooling of data for combined sexes may mask certain growth patterns such as enhanced growth rates following sexual transition and could lead to errors in the predictions obtained from standard yield models (Bannerot et al., 1987). Thus, subsequent studies should consider the effects of an alternative reproductive strategy on population parameters and the predictions for management of these species in Trinidad and Tobago.

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