

Abstract.—The red hind *Epinephelus guttatus*, a grouper of commercial importance in the central western Atlantic, is believed to be overexploited in a number of areas. Red hind taken by fish trap and hook-and-line in western Puerto Rico and the U.S. Virgin Island of St. Thomas were aged using sectioned otoliths (sagittae). Ages were validated by marginal increment analysis for fish ages 1–10 yr, and by a field study involving oxytetracycline injection for fish ages 1–4; a single opaque and translucent zone (viewed under transmitted light) is deposited annually. For Puerto Rico, the von Bertalanffy growth function (VBGF) was $L_t = 514.5 (1 - e^{-0.101(t+2.94)})$. Back-calculated mean fork lengths ranged from 163 mm at age-1 yr, to 448 mm at maximum age-17. For St. Thomas, the VBGF was $L_t = 601.0 (1 - e^{-0.071(t+4.69)})$. Back-calculated mean fork lengths ranged from 194 mm at age-1, to 470 mm at maximum age-18. Sex and stage of sexual maturation were determined for a subsample of aged fish from Puerto Rico. Fifty percent of females had attained sexual maturity by age 3 yr. Ages of females were 1–9 yr; males, 2–17 yr, and individuals undergoing sexual transition from female to male, 3–7 yr. The male to female sex ratio was 1:2.6. The occurrence of sexually-transitional individuals, as well as significant differences between the sexes in both size and age, confirm protogynous hermaphroditism for fish from Puerto Rico.

Age and growth of red hind *Epinephelus guttatus* in Puerto Rico and St. Thomas

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The red hind *Epinephelus guttatus* is a serranid of considerable commercial importance throughout the Caribbean, the Bahamas, and Bermuda (Burnett-Herkes 1975, Mahon 1987). In Puerto Rico and the U.S. Virgin Islands, this species is one of the most-frequently reported groupers in commercial landings. It is taken by hook-and-line, fish trap, and speargun, over the insular shelf to a depth of about 80 m.

Grouper are relatively long-lived and slow-growing fishes. These characteristics, combined with the protogynous sexual pattern (female to male sex change) reported for many grouper, and intensive fishing over short-term traditional spawning aggregations, render grouper species especially vulnerable to overexploitation (Bannerot et al. 1987, Manooch 1987, Ralston 1987, Shapiro 1987, Bohnsack 1989).

There are indications that red hind resources of Puerto Rico and the U.S. Virgin Islands are being overexploited. Commercial grouper landings reported in Puerto Rico have declined consistently and substantially over the last decade, from 386 mt in 1978 to 47 mt (of which 38% were red hind) in 1990 (Matos and Sadovy 1989, Sadovy In press, Sadovy and Figuerola 1992). Yield-per-recruit analyses indicate growth overfishing (harvesting at too small a size to maximize potential yield) in western

Puerto Rico (Stevenson 1978, Sadovy and Figuerola 1992). All known annual spawning aggregations in both Puerto Rico and St. Thomas are heavily exploited. In addition, recent length-frequency data from commercial catches in St. Thomas indicate that mean length declined substantially between 1984 and 1988 (Beets and Friedlander 1992), although it is not clear to what extent this decline is attributable to overfishing, or is related to annual variation in recruitment (Appeldoorn et al. 1992), or a combination of the two.

Little is known of the life history of the red hind. Previous studies on age and growth in this species have been conducted in Bermuda using whole otoliths (Burnett-Herkes 1975), and in Jamaica using length-frequency analysis (Thompson and Munro 1974). However, neither study is recent and neither validated the ageing techniques. The sexual pattern is reported to be protogyny in Bermuda (Smith 1959, Burnett-Herkes 1975), and protogyny is also indicated for Puerto Rico stocks (Shapiro et al. unpubl. data). The objectives of this study were to determine age and growth of the red hind in two heavily-exploited areas—western Puerto Rico and St. Thomas, U.S. Virgin Islands—and to confirm sexual pattern. This information is necessary to allow stock assessments to be made for this species, and to permit the development of a management policy for the red hind in the region.

Methods

Samples of *Epinephelus guttatus* were obtained from local fishermen and from Fisheries Research Laboratory (FRL) research programs using hook-and-line and arrowhead fish traps (3.2 cm (1.25 in.) galvanized mesh). Monthly collections were made between September 1987 and January 1989 with a minimum of 80 fish for most months from Puerto Rico. Smaller monthly samples from February 1988–January 1989 were received from St. Thomas, which lies on the same geological platform. Fish from St. Thomas were taken by hook-and-line and by fish trap (3.81 cm (1.5 in.) galvanized mesh).

For each fish, the weight (whole weight to nearest gm) and length (fork length (FL) and standard length (SL) to nearest mm) were measured. Otoliths (sagittae) were extracted, washed, and stored dry prior to processing. Preliminary work determined these calcareous structures to be more suitable than other calcareous structures for ageing purposes: dorsal spines exhibited growth lines but the central portion was often eroded resulting in an incomplete growth history, and scale markings were irregular and thus considered unreliable for ageing. Gonads in good condition were removed whenever possible, fixed in Davidson's fixative (Yevich and Barszcz 1981), embedded in paraffin, sectioned at 8 μ m, and stained with hematoxylin and eosin.

Examination of whole otoliths under transmitted light revealed alternating opaque and translucent zones (terminology follows that of Wilson et al. 1983). To count the zones, however, otoliths had to be sectioned. Preliminary sectioning in two planes (frontal and transverse; $N=20$ otoliths in each plane) established that transverse sections most clearly revealed growth zones. For sectioning, otoliths were mounted with glue, using a hot glue gun, on small cards, and sectioned through the focus with a single 7.2 cm (3 in.) diameter, low-concentration diamond blade on a Buehler Isomet low-speed saw. From each otolith, three sections of 0.36–0.43 mm were mounted on glass slides using Flo-Texx mounting medium.

Otolith width (OW) of a sample of unsectioned otoliths from a wide size-range of fish was measured to describe the OW/FL relationship. Measurements of otolith sections were made from the point where the sulcus meets the focus to the dorsal margin of the otolith (the region of most rapid growth) and to the proximal edge of each opaque zone. Measurements were also made from the distal edge of the outermost (opaque) zone to the dorsal margin for marginal increment analysis. Total number of opaque zones was noted. Measurements were made with an ocular micrometer, to the nearest micrometer unit (where

1 mm = 32 micrometer units). Each otolith was read twice. When readings disagreed by more than one opaque zone, the otolith was eliminated. Readings of a subsample of otoliths from Puerto Rico, of a wide range of ages and size-groups, were also made by an independent researcher.

To validate the temporal significance of opaque zones, a field study was undertaken. Individuals were captured by hook-and-line baited with squid from a 30 \times 30 m area on a shallow (7 m) relatively-unfished reef known as "El Negro," 6 km off western Puerto Rico. The study site was visited over a 15-month period between April 1988 and June 1989. Individuals were tagged with a numbered FLOY anchor tag inserted into the dorsal musculature, and/or with FLOY abdominal tags for identification. Each fish was measured (FL) and injected with a dosage of 100 mg/kg body weight of Terramycin 100 (Pfizer) (1 mL contains 100 mg oxytetracycline-OTC-hydrochloride), and released. The dosage necessary to produce a visible mark under longwave ultraviolet light was established by preliminary tests (50 and 100 mg/kg body weight were tested; 50 mg/kg body weight did not consistently leave OTC marks) and the correct dosage determined on-site from a weight/FL relationship. Fish recaptured were measured and the otoliths examined for opaque zone formation following deposition of the OTC time marker.

Data were analyzed separately for Puerto Rico and St. Thomas using Lotus 1-2-3 and Basic Fishery Science Programs (Saila et al. 1988). The Kolmogorov-Smirnov two-sample test and the t -test were used to compare size-frequency distributions and mean size, respectively (Sokal and Rohlf 1981). Weight (W) on FL regressions were calculated using the relationship $W = aFL^b$. The SL:FL and OW:FL regressions were determined. The Lee method (Carlander 1981) of back-calculating body length from prior annuli was used:

$$L_i = a + [(L_c - a) (O_i/OR)],$$

where: L_i = length at time of i th annulus formation
 a = intercept
 L_c = length at time of capture (FL)
 O_i = otolith radius at time of i th annulus formation
 OR = otolith radius at time of capture.

This method requires knowledge of the relationship between OR along the line of measurement and FL . The constant a is obtained from this relationship and used in Lee's formula.

Growth was assumed to conform to the von Bertalanffy growth function (VBGF) (Ricker 1975). This

was calculated from the Saila et al. (1988) statistical package (FISHPARM program using Marquadt's non-linear least-squares method) and fitted to mean back-calculated lengths-at-age. The VBGF is

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

where L_t = length at age t
 L_∞ = asymptote of the growth-in-length curve
 K = Brody growth coefficient
 t = age of the fish
 t_0 = the theoretical origin of the growth curve, i.e., age at which fish would have zero length if it had always grown in a manner described by the equation.

To establish chronological age at the time of first opaque zone formation, data on the early growth of juvenile red hind were assembled from field collections and observations taken over 9-month periods following spawning in January of 1985 and 1987 (Sadovy, unpubl. data). Since spawning occurs over a limited period, during, at most, 2 months each year (Erdman 1976, Beets and Friedlander 1992, Shapiro et al. In press), and settlement may be assumed to occur between 3 weeks to 2 months after spawning (Colin et al. 1987), growth rates of individuals in the months following settlement could be estimated.

Results

Samples

Of 1684 *Epinephelus guttatus* collected from Puerto Rico, otoliths were sectioned from 1098. Opaque and translucent zones were detectable in almost all otolith sections. When zones lacked sufficient definition for focus-to-ring measurements, the otoliths were discarded as unsuitable for use in calculating growth parameters, although some were used to assign ages to sexed fish by counts of opaque zones. A total of 624 (63%) otoliths were used to count growth zones and for focus-to-ring measurements. Of these, a subsample of 73 otoliths was read by an independent researcher; only one was rejected because of a discrepancy of more than one zone compared with our readings. Of the 501 St. Thomas samples, otoliths were sectioned from 490, and 162 (33%) were judged to be sufficiently clear for analysis; it is not known why otolith legibility was so low for St. Thomas samples.

Size-frequency distributions of all fish collected in Puerto Rico and in St. Thomas, and the subsamples used for analysis of otoliths from each location, are shown

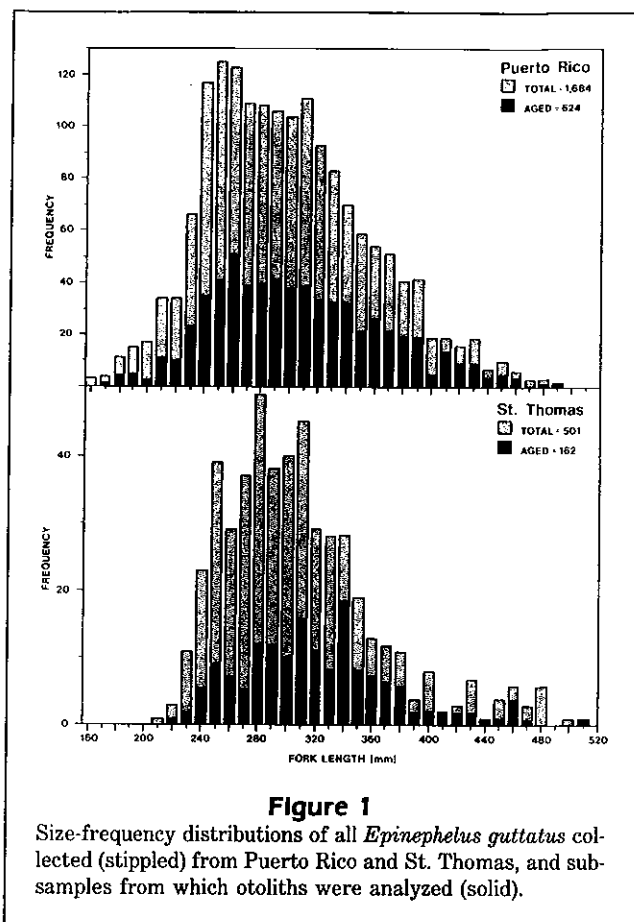


Figure 1
 Size-frequency distributions of all *Epinephelus guttatus* collected (stippled) from Puerto Rico and St. Thomas, and subsamples from which otoliths were analyzed (solid).

in Figure 1. For Puerto Rico, size-frequency distributions of individuals and subsamples used for age determination did not differ significantly (Kolmogorov-Smirnov: $D=0.043$, NS). This confirmed our impression that illegible otoliths occurred at all fish sizes and ages, and affirmed that their elimination introduced no bias to the calculation of growth parameters. For St. Thomas, however, the distributions differed significantly ($D=0.150$, $p<0.05$). Therefore, growth parameters derived for St. Thomas should be treated with caution.

Frequency distributions of the distance from the focus to each opaque zone in Puerto Rico collections are shown in Figure 2. Relationships of SL:FL and W:FL were established for each location.

Puerto Rico:

$$\begin{aligned} \text{FL} &= 3.86 + 1.2044 \text{ SL} \quad (r^2 \text{ 0.99; } N \text{ 227}) \\ \text{Log W} &= -5.21 + 3.1422 \text{ Log FL} \quad (r^2 \text{ 0.97; } N \text{ 1619}) \end{aligned}$$

St. Thomas:

$$\begin{aligned} \text{FL} &= 24.49 + 1.1101 \text{ SL} \quad (r^2 \text{ 0.98; } N \text{ 494}) \\ \text{Log W} &= -4.68 + 2.9402 \text{ Log FL} \quad (r^2 \text{ 0.92; } N \text{ 493}) \end{aligned}$$

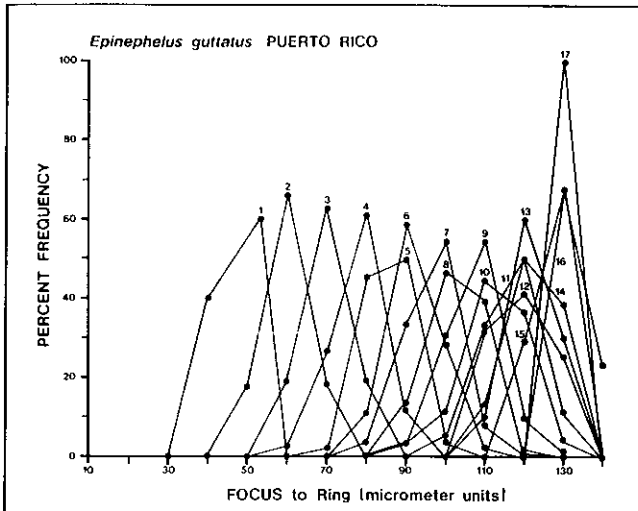


Figure 2

Frequency distributions of the distance from focus to proximal edge of each opaque zone (1-17) in sectioned sagittae of *Epinephelus guttatus* from Puerto Rico.

Validation

Marginal increment analysis Mean marginal increments for Puerto Rico fish were plotted on a monthly basis for annuli I-VI individually, and combined for annuli VII-X because of low monthly sample sizes for these older age-groups (Fig. 3). These data indicate that, at least for annuli II-V, the opaque zone begins to form between about April and May and is a true annulus. For annulus VI, the zone is laid down later, between May and July. For annuli VII-X combined, opaque zones are apparently deposited annually between May and July.

Since sample sizes from St. Thomas were too low for marginal increment analysis by individual age-group, otoliths from all age-groups were combined and plotted on a monthly basis by the percent of sections that lacked a marginal increment. These data indicate that the time of opaque zone formation (i.e., spring/summer) is similar for both Puerto Rico and St. Thomas (Fig. 4). A possible 'pseudoannulus' was detected in 74 (12%) of sectioned otoliths. This was a wide, weakly-discernible band always located between the focus and the first annulus. It occurred sporadically in fish of all sizes.

Field validation study Of a total of 139 fish tagged, injected, and released, 8 females from age-classes 1-4 were recaptured 5-16 months following tagging. Mean monthly growth rates for recaptured individuals from Puerto Rico measured 1-8mm (Table 1). One individual (#00038) was recaptured in February 1991, 18km from the tagging site on an offshore bank, a known spawn-

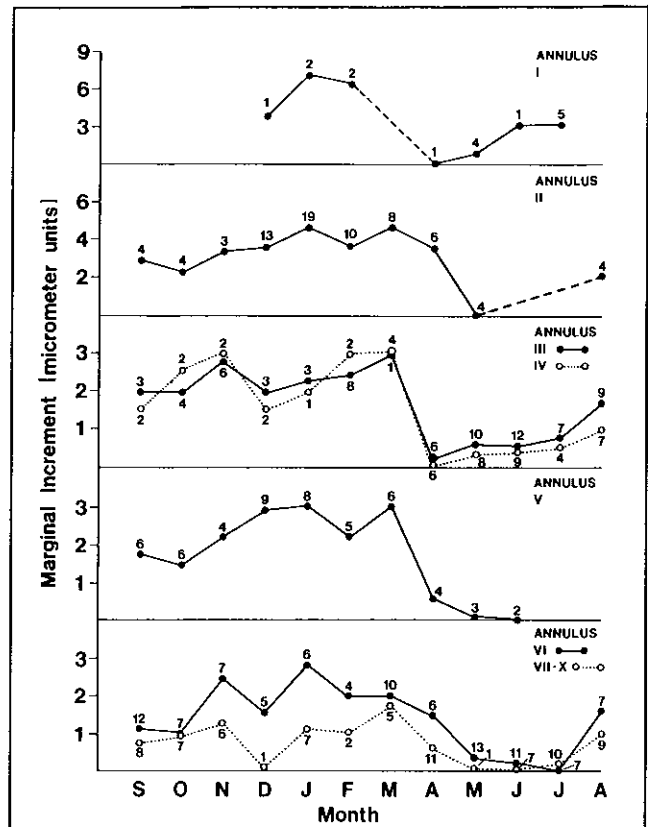


Figure 3

Marginal increment analyses for annuli I-X for *Epinephelus guttatus* from Puerto Rico (1 micrometer unit = 0.031 mm). Numbers above plots are sample sizes. Dashed lines connect samples separated by more than one month.

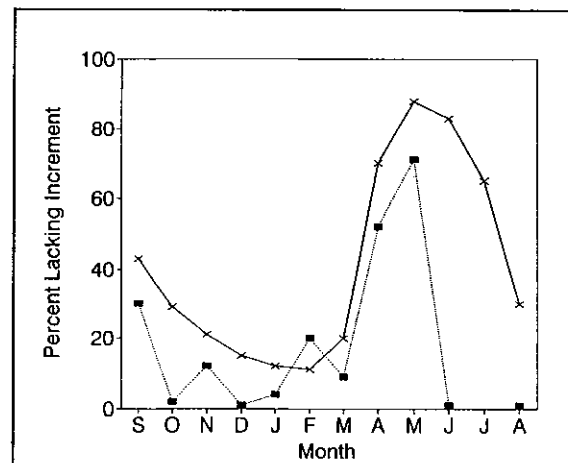


Figure 4

Percentage of otolith sections lacking a marginal increment for *Epinephelus guttatus* from Puerto Rico (solid line) and St. Thomas (dashed line) for age groups 1-10.

Table 1

Temporal significance of opaque growth zones in otoliths of *Epinephelus guttatus* from Puerto Rico, based on OTC-marked/recaptured fish. OR = otolith radius; MI = marginal increment; OTC = oxytetracycline mark.

Tag no.	Date (D/M/Y) Capture Recapture	FL (mm) Capture Recapture	Days in field	Measurements (32 micrometer units = 1 mm)							OR	MI	No. of opaque zones
				Focus to ring					OTC				
				1	2	3	4						
00094	01/06/88 31/10/88	163 203	152	37*	—	—	—	—	¹ 46	55	4	1	
00078	25/05/88 04/05/89	127 151	344	45*	59	—	—	—	¹ 52	63	0	2	
00076	01/06/88 14/02/89	202 231	258	40	52	61	—	—	² 65	72	4	3	
00468	13/05/88 20/03/89	210 220	311	38	54	60	—	—	² 68	73	5	3	
00418	02/06/88 31/10/88	214 220	151	34	51	62*	—	—	¹ 64	71	0	3	
00385	19/08/88 10/02/89	218 248	175	39	50	69	—	—	³ 60	70	0	3	
⁴ 00038	11/10/89 14/02/91	261 289	491	43	61	75	—	—	³ 72	85	3	3	
00426	08/06/88 07/02/89	287 317	244	45	60	73	87	—	² 90	95	4	4	

¹OTC mark lies within opaque zone indicated by asterisk.

²OTC mark lies at junction of opaque and translucent zones.

³OTC mark lies within translucent zone.

⁴Fish originally tagged June–December 1988; inner OTC mark 52⁽⁹⁾. Retagged 11/10/89 (only retag data presented).

Table 2

Mean back-calculated and observed fork lengths (mm) at time of opaque zone formation (yr) for age-groups 1–17 of 624 *Epinephelus guttatus* from Puerto Rico.

Age-group	N	Mean length at capture	SD	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
1	19	184	47	161																	
2	97	247	21	168	213																
3	90	256	23	162	203	234															
4	52	272	26	159	195	226	253														
5	87	306	30	163	205	237	263	286													
6	126	321	33	165	207	237	262	283	303												
7	52	342	42	163	205	236	262	284	305	325											
8	29	353	34	169	209	236	260	283	304	320	336										
9	26	374	36	160	209	241	269	290	310	327	340	357									
10	27	393	32	170	213	244	271	293	312	329	346	361	374								
11	5	413	41	163	211	247	270	298	315	333	349	366	382	399							
12	4	416	30	160	194	226	257	283	302	321	335	352	366	382	394						
13	2	422	17	168	219	250	275	296	313	334	347	360	372	384	399	410					
14	5	448	31	172	212	247	278	304	323	340	354	368	383	409	417	432					
15	0	—	—																		
16	1	448	—	155	213	238	262	277	289	308	332	353	372	387	393	405	414	424	436		
17	2	458	46	159	216	247	271	293	312	323	336	348	362	380	395	406	416	431	440	448	
Back-calculated mean lengths (weighted)				164	206	236	262	286	306	326	342	359	375	390	401	412	426	429	439	448	
Growth increments					42	30	26	24	20	20	16	16	16	15	11	11	14	3	10	9	

ing aggregation area. To reach the bank, this fish must have crossed water of at least 194 m depth, a substantial depth for similar-sized individuals of this species (Sadovy et al., unpubl. data).

During the tagging study, significant data loss occurred; in approximately 60% of tagged fish resighted, the identifying number of the dorsal tag had detached, leaving behind a monofilament anchor partially embedded in dorsal musculature. On the other hand, resightings of fish marked with abdominal tags indicated that all had retained both the numbered tag anchor and the attached color streamer.

Data for age-groups of recaptured fish indicated that no more than one opaque zone is deposited annually, although sample size was limited. Opaque zone formation had begun in or after February, had terminated prior to August, and occurred somewhat later in the year in older age-groups.

Recaptures were initiated as early as 5 months after tagging because individuals typically disappeared from the immediate study site within a few months of capture. Results covering less than a 12-month field period should be treated with caution, although all results were consistent with the marginal increment analysis in terms of both the temporal nature of opaque zones and the time of their annual deposition.

Age and growth

For Puerto Rico, the FL/OR relationship is

$$FL = 33.2180 + 3.0743 OR \quad (r^2 \ 0.76; N \ 624).$$

Table 2 shows the mean back-calculated lengths for ages 1–17 years from 624 fish. The following growth parameter estimates were obtained from the von Bertalanffy growth function (with asymptotic SE in parentheses):

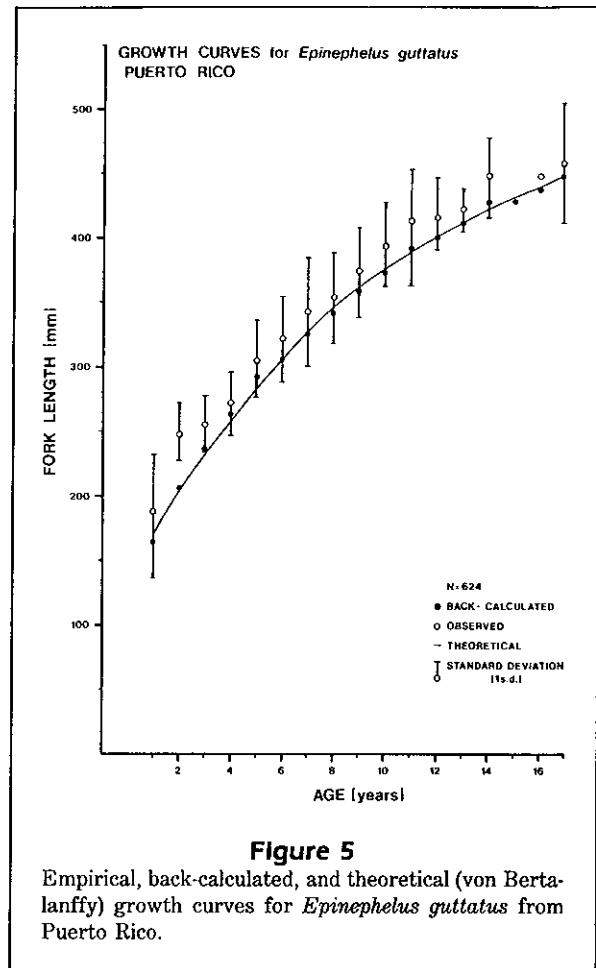
$$\begin{aligned} L_{\infty} &= 514.5 \text{ mmFL} \quad (6.29) \\ K &= 0.1013 \quad (0.003765) \\ t_0 &= -2.944 \quad (0.1357). \end{aligned}$$

Figure 5 shows empirical mean lengths and their standard deviations, as well as back-calculated and theoretical (VBGF) growth curves, for Puerto Rico.

For St. Thomas the FL/OR relationship is

$$FL = 94.7206 + 2.4757 OR \quad (r^2 \ 0.68; N \ 162).$$

Table 3 shows the mean back-calculated lengths for age-groups 1–18 from 162 fish. The following growth parameter estimates were obtained from the von Bertalanffy growth function (with asymptotic SE in



parentheses):

$$\begin{aligned} L_{\infty} &= 601.0 \text{ mmFL} \quad (32.82) \\ K &= 0.0705 \quad (0.009954) \\ t_0 &= -4.690 \quad (0.5920). \end{aligned}$$

Figure 6 shows the empirical mean lengths and their standard deviations, as well as back-calculated and theoretical growth curves, for St. Thomas.

For Puerto Rico, the OW/FL relationship is

$$OW = 1.4205 + 0.0108 FL \quad (r^2 \ 0.93; N \ 315; \text{Fig. 7}).$$

For St. Thomas, the OW/FL relationship is

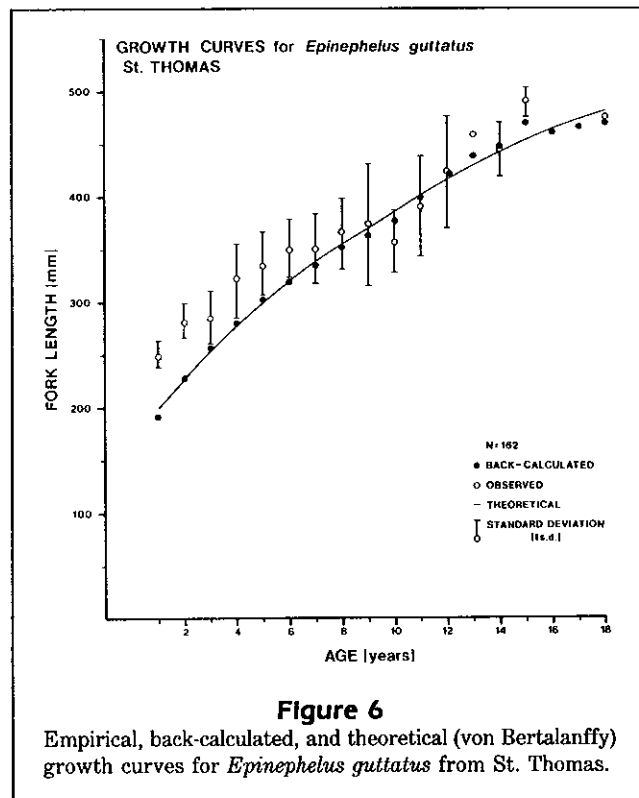
$$OW = 0.5591 + 0.0049 FL \quad (r^2 \ 0.93; N \ 101).$$

When mean back-calculated fork lengths for annuli I–V for age-groups 1–14 from Puerto Rico and St. Thomas are plotted (Fig. 8), two points are worthy of note. If regressions for each annulus are calculated for all available ages up to age-group 14, all are statistically

Table 3

Mean back-calculated and observed fork lengths (mm) at time of opaque zone formation (yr) for age-groups 1-18 of 162 *Epinephelus guttatus* from St. Thomas.

Age-group	N	Mean length at capture	SD	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
1	7	249	12	204																		
2	10	260	17	195	232																	
3	39	280	25	190	229	259																
4	10	284	28	185	213	243	265															
5	16	319	28	195	229	260	286	308														
6	27	335	27	195	228	255	278	298	316													
7	11	348	29	194	227	255	278	297	317	333												
8	13	362	29	195	230	258	282	303	320	333	349											
9	9	370	55	195	226	252	275	296	315	331	343	358										
10	5	356	28	184	212	238	261	279	296	312	324	333	345									
11	5	391	45	195	228	253	279	300	317	332	345	355	367	378								
12	3	424	51	203	242	273	294	311	329	346	358	375	388	401	411							
13	1	460	—	206	234	270	290	332	348	365	382	396	410	424	438	452						
14	3	442	22	222	246	269	291	318	339	355	368	378	391	399	412	420	430					
15	2	492	12	215	263	290	316	343	362	378	389	405	421	434	450	460	469	478				
16	0	—	—																			
17	0	—	—																			
18	1	475	—	192	217	248	273	299	324	350	368	386	401	414	427	432	439	452	460	465	470	
Back-calculated mean lengths (weighted)				194	228	256	279	301	318	335	349	362	377	400	423	438	445	469	460	465	470	
Growth increments					34	28	23	22	17	17	14	13	15	23	23	38	7	24	-9	5	5	



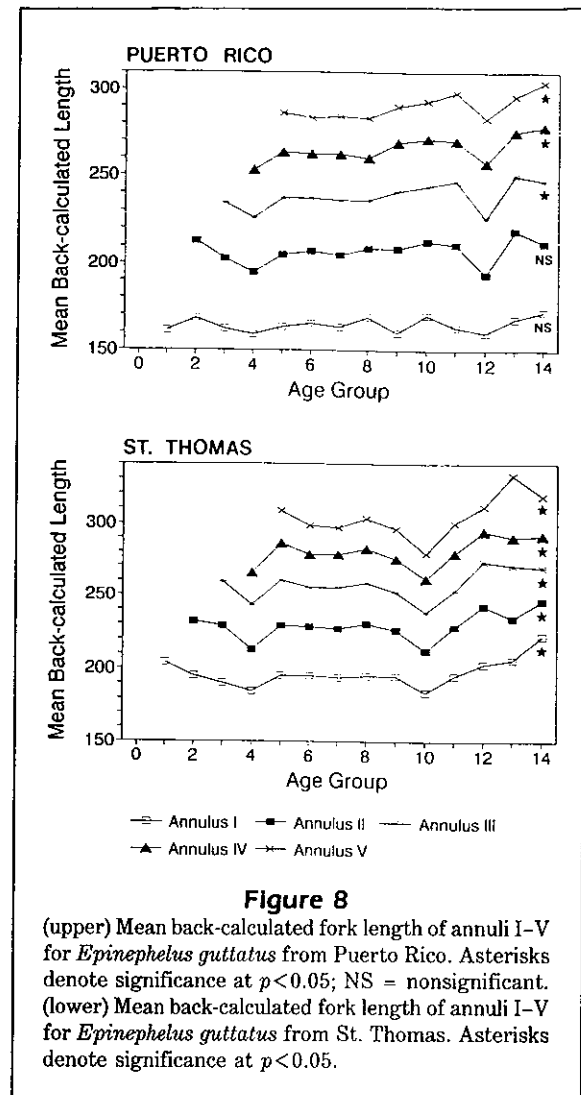
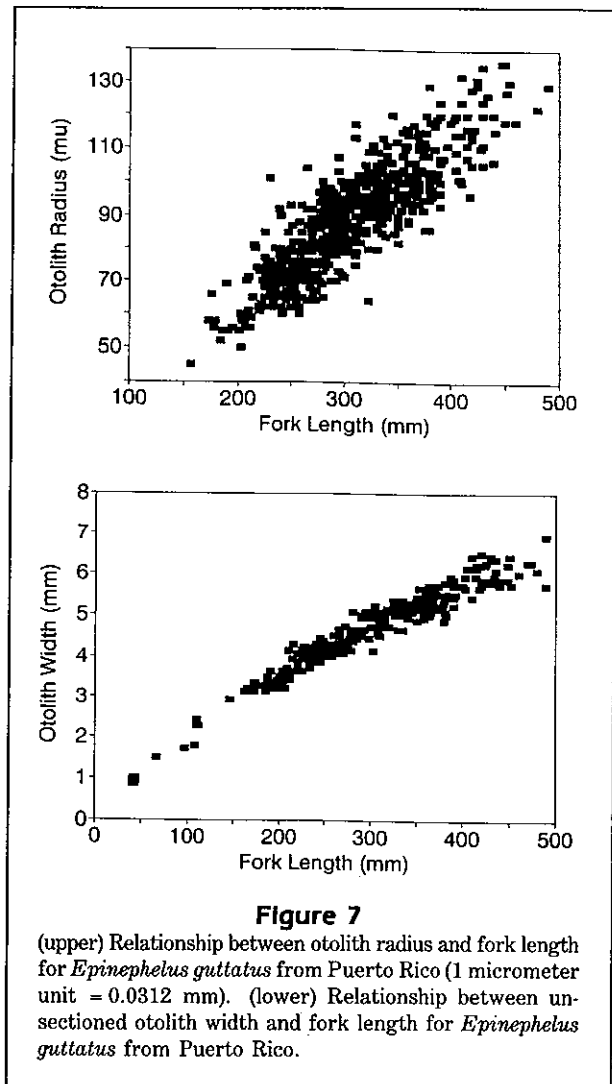
significant ($p < 0.05$), with the exception of annuli I and II for Puerto Rico. Also of note are two distinct depressions in back-calculated mean lengths for each geographic location. For Puerto Rico these are indicated at age-groups 4 and 12, and for St. Thomas at age-groups 4 and 10. These points will be addressed in the discussion.

Data on growth during the months following spawning indicate rapid growth from the time of settlement in February or March at ~40 mm FL ($N = 29$), to 60 mm FL in April/May ($N = 3$), 108 mm ($N = 2$) in August, and 115 mm ($N = 4$) in October.

Age, sex, and size

A total of 186 individuals from Puerto Rico were sexed, by histological examination of gonads, and aged. Of these, 131 were female and 50 were male; 5 were considered to be in sexual transition between female and male, with gonads consisting of degenerating sexually-mature (i.e., vitellogenic) ovarian tissue and scattered areas of spermatogenic tissue exhibiting various stages of spermatogenesis (Sadovy and Shapiro 1987). All males exhibited testes with an ovarian-like configuration and lumen (Sadovy and Shapiro 1987).

Mean observed FL, standard deviation, and sample size by sex and age-class from Puerto Rico are shown



in Table 4. Fork length at time of capture (i.e., observed FL) did not differ significantly between the sexes for age-groups 2–8 (Table 4). However, both age- and size-frequency distributions from both Puerto Rico and St. Thomas differed significantly by sex (age: $D = 0.593$, $p < 0.01$; size: $D = 0.576$, $p < 0.01$) (Fig. 9).

Females were found at ages 1–9, males at ages 2–17, and individuals undergoing sexual transition at ages 3–7 (Table 4). No sexually-mature individuals were detected below age 2 years. Fifty percent of females had attained sexual maturity by age 3.

Discussion

Validation and formation of opaque zones

Opaque zones incrementally deposited in the sagittae of the red hind *Epinephelus guttatus* were validated

as annual in this study, both by marginal increment analysis and by a field study involving the marking of otoliths by OTC. Although the possibility of bi- or multi-annual growth lines (Deelder 1981, Lee et al. 1983) for fish aged 11 years and over could not be discarded, these age-groups constituted a small percentage of sampled individuals; hence, the validation may be applied confidently to the exploited segment of red hind stocks in the region.

It is not known what causes the formation of opaque and translucent zones in this species. However, since zones are found in both adults and juveniles, they are clearly not caused exclusively by spawning activity (Nekrasov 1980). Opaque zone formation has been proposed to be associated with low somatic growth rates, and translucent zones with high growth rates, in the white grunt *Haemulon plumieri* (Sadovy and Severin 1992). A similar relationship is proposed for the red

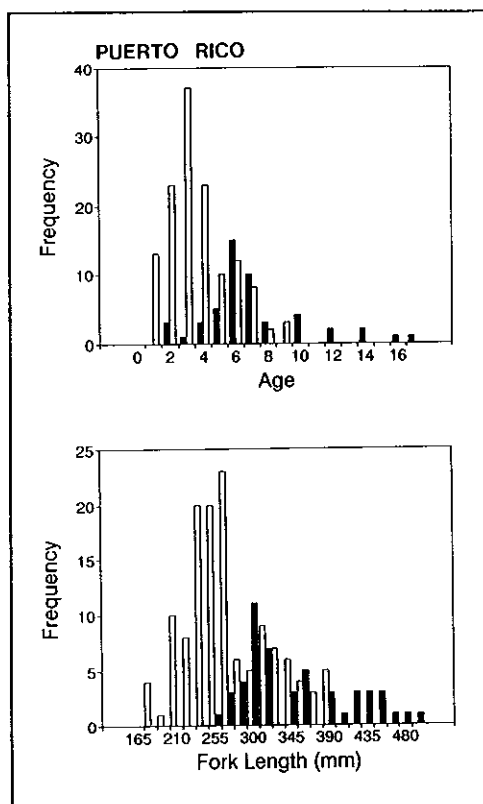


Figure 9

(upper) Age-frequency distributions of female (stippled) and male (solid) *Epinephelus guttatus* from Puerto Rico. (lower) Size-frequency distributions of female (dotted) and male (solid) *Epinephelus guttatus* from Puerto Rico.

hind (Sadovy and Severin, unpubl. data). Since time of opaque zone formation was earlier in the year in younger than in older fish, zone formation is unlikely to be caused by a simple environmental factor acting directly and equally on all individuals. Time of opaque zone formation is February–July, which is similar to that reported for four other groupers of the genus *Epinephelus* from the western Atlantic (Table 5). The pattern of earlier annual opaque zone formation in younger individuals noted in our study was also reported in otoliths from *E. morio* (Moe 1969) and *Mycteroperca microlepis* (Collins et al. 1987), and in pike *Esox lucius* (aged using cleithra; Casselman 1983).

Data on growth of red hind in the months following settlement indicate rapid growth from the time of settlement at ~40 mm FL ($N=29$), to 115 mm FL the following October. These data indicate that the first opaque zone, which is laid down between March and April at a back-calculated 164 mm FL (SD 18 mm) in Puerto Rico and 194 mm FL (SD 17 mm) in St. Thomas, represents an age 1+ year fish (13–15 months old, depending on month of spawning).

Growth parameters and longevity

Red hind in Puerto Rico and St. Thomas are long-lived and attain their maximum size slowly, following fast growth during the first year. Thompson and Munro (1974), using length-frequency analysis, calculated $L_{\infty} = 520$ mm FL for Jamaica–Pedro Bank fish, and $L_{\infty} = 500$ mm FL for Jamaica–Port Royal fish. Burnett-Herkes (1975),

Table 4

Mean observed fork length (mm) and standard deviation for male and female red hind, *Epinephelus guttatus*, by age-group. Fish from Puerto Rico collected September 1987–September 1988 (* $p < 0.05$). NS = nonsignificant.

Age	Observed fork length (mm)						Student's t	Transitional fish	
	Female			Male				FL	N
	\bar{x}	SD	N	\bar{x}	SD	N			
1	196.3	16.3	13	—	—	—	—	0	
2	238.7	20.6	23	253.7	34.2	3	1.1076 NS	0	
3	251.5	18.6	37	301.0	—	1	0.1410 NS	275 1	
4	267.2	28.0	23	280.7	10.5	3	0.8150 NS	278 1	
5	307.2	28.4	10	288.0	7.3	5	1.4621 NS	0	
6	344.9	35.8	12	322.2	30.4	15	1.7823 NS	315 1	
7	340.6	25.9	8	336.6	49.4	10	0.2066 NS	258; 380 2	
8	362.5	17.5	2	368.7	50.4	3	0.2536 NS	0	
9	326.7	12.5	3	—	—	0	—	0	
10	—	—	—	418.0	14.9	4	—	0	
11	—	—	—	—	—	0	—	0	
12	—	—	—	440.0	10.0	2	—	0	
13	—	—	—	—	—	0	—	0	
14	—	—	—	470.0	10.0	2	—	0	
15	—	—	—	—	—	0	—	0	
16	—	—	—	448.0	—	1	—	0	
17	—	—	—	490.0	—	1	—	0	
Total	268.0	50.0	131	342.0	65.0	50	8.1597*	301 5	

Table 5
Caribbean and western Atlantic *Epinephelus* spp. aged by whole or sectioned otoliths.

Species	Growth parameters*			Time of opaque zone formation	Max. age (yr)	Source
	L_{∞} (mm FL)	K	t_0 (yr)			
<i>E. nigritus</i>	2394	0.054	-3.616	April-May	41	Manooch and Mason 1987
<i>E. niveatus</i>	1320	0.087	-1.012	May-July	17	Moore and Labisky 1984
<i>E. niveatus</i>	1255	0.074	-1.920	May-July	17	Matheson and Huntsman 1984
<i>E. drummondhayi</i>	967	0.130	-1.010	April-June	15	Matheson and Huntsman 1984
<i>E. morio</i>	928	0.113	0.091	—	14+	Melo 1975 (cited in Manooch 1987)
<i>E. morio</i>	792	0.179	-0.449	March-July	25+	Moe 1969
<i>E. guttatus</i>	601	0.071	-4.690	March-June?	18+	This study; St. Thomas
<i>E. guttatus</i>	515	0.101	-2.944	February-July	17+	This study; Puerto Rico
<i>E. guttatus</i>	507	0.180	-0.440	—	17+	Burnett-Herkes 1975; also used length-frequency data

* L_{∞} = asymptote of the growth-in-length curve; K = Brody growth coefficient; t_0 = theoretical origin of von Bertalanffy growth curve (Ricker 1975).

using whole otoliths and length-frequency analyses for ageing, reported $L_{\infty} = 507$ mm FL in Bermuda. The largest fish sampled in the present study were 490 mm FL in Puerto Rico and 504 mm FL in St. Thomas. In several years of intensive sampling of thousands of red hind from local commercial landings, Fisheries Research Laboratory (FRL) data recorded <2% of individuals >500 mm FL (FRL, unpubl. data). These data reflect asymptotic lengths established in the present study. Randall (1983) reported the largest West Indian specimen collected to be 673 mm FL, and Smith (1971) reported the largest fish he examined to be 510 mm SL (618 mm FL using the above FL/SL relationship).

Growth parameters obtained using otoliths as the ageing structure for western Atlantic species of the genus *Epinephelus* are shown in Table 5. The data for *E. guttatus* in Puerto Rico and St. Thomas fall within the range of values of L_{∞} , K, and maximum age reported for western Atlantic grouper. A maximum of 17 growth zones in Puerto Rico and 18 growth zones in St. Thomas were recorded. We consider the estimated longevity of 17+ and 18+ to be reasonable for commercially-taken red hind in Puerto Rico and St. Thomas, respectively. Luckhurst et al. (1992) recorded 22 (± 1) opaque zones in an unusually-large 720 mm FL individual from Bermuda.

Lengths-at-capture were consistently higher than back-calculated lengths for each age-group (Figs. 5, 6). The higher observed mean fork lengths generally reflect additional growth between previous ring formation and time of capture. However, the notably high observed mean FL of ages-1 and -2 fish for both Puerto Rico and St. Thomas may be due, in part, to selection

by the fishery of the largest fish in these younger age-groups. Similar selection was also reported for the first two age-classes in *E. morio* (Moe 1969) and may be especially common in longer-lived, slower-growing species, such as grouper (Bannerot 1984). When sampling is biased towards larger individuals of young year-classes, there may be artificial depression of K in the VBGF (Ricker 1975). A downward bias would generally produce conservative management advice in terms of justifying imposition of minimum size regulations based on future returns to the fishery (Bannerot 1984).

The relationship between FL and OR for both locations is somewhat weaker than in other studies of fish age and growth. Since the OW/FL relationships for otoliths from both locations are strong, this indicates that variability is introduced by the position on the sectioned otolith selected for measurement and counting of opaque zones, rather than by a poor relationship between body length and otolith size (Fig. 7).

The regressions for mean back-calculated fork lengths of annuli I-V of age-groups 1-14 for Puerto Rico and St. Thomas are statistically significant, with two exceptions (Fig. 8). Such a trend could suggest a reverse "Rosa-Lee" phenomenon, indicating enhanced survivorship of fast-growing fish (Ricker 1975). If this were true, it would result in an upward bias of the parameter K in the VBGF. However, sample sizes for individuals above age-group 10 are very low, and regressions for age-groups 5-10 are not significant, with the exception of annulus II for Puerto Rico. Since these age-groups comprise the bulk of commercial landings, we believe that bias to estimates of growth parameters derived in the present study is negligible. Furthermore, since a similar increase is apparent in most age-groups

below age-group 4, there is clearly no consistent relationship between growth rate and mortality.

The depressions in back-calculated mean lengths (Fig. 8) apply to years 1983–84 (age-group 4) and 1975–76 (age-group 12) for Puerto Rico, and 1984 (age-group 4) and 1978 (age-group 10) for St. Thomas. In the case of older age-classes, small sample sizes could have produced sampling errors. However, we believe that in the case of 1984, this pattern is unlikely to be the result of sampling artifacts. Possible explanations for lower mean back-calculated lengths in both locations include environmental factors, such as unusually low temperatures or reduced food availability, or alterations in fishing effort and associated demographic changes. We know of no changes in fishing effort or gear during the early 1980s at either location. Reduced environmental temperatures or food availability may have caused age-1 and -2 fish to experience a decrease in growth rate that carried over into later years. Interestingly, catch curves developed from the same data set indicate a particularly low recruitment into the fishery of age-4 fish in 1984 (Sadovy and Figuerola 1992). This trend in the catch curves is strikingly similar for both locations, strongly suggesting a region-wide phenomenon. Poor recruitment into the fishery of a young age-class could result from slow growth early in life of individuals of that cohort.

Examination of temperature records for the region indicates that the winter of 1984 was the first since that of 1975 in which the mean minimum temperature dropped below 26°C (lat. 14.7°–18.2°) (Atwood and Hendee In press). In summary, we suggest that lower temperatures may have retarded growth in young individuals and that this reduction in size-at-age early in life was carried through the growth history of the animal.

Age and sex

Among sexed individuals, the majority (80%) of females were ages 1–5, and the males ages 2–10. Empirical mean lengths for age-groups 2–8 did not differ by sex. Moe (1969) also found the empirical growth curves of the sexes of *E. morio* to be similar, indicating that there are no marked differences in growth between the sexes or sexual phases of an individual. The combination of histological data, especially the presence of transitionals, size/age frequency distributions, and a female-biased sex ratio, confirm protogyny for this species in Puerto Rico. However, the presence of males as young as the youngest mature female indicates that at least some males may develop directly from a juvenile phase without passing through an initial functional female phase.

The red hind and fishery management

The condition of growth overfishing in the red hind (Sadovy and Figuerola 1992), and the general vulnerability of grouper species to fishing pressure, indicate the urgent need for management, stock monitoring, and assessment throughout its geographic range. In particular, given the apparent importance of spawning aggregations for annual reproductive output in the red hind (Bohnsack 1989; Shapiro 1987), and the intensity with which these are exploited locally (Sadovy, unpubl.), the possibility of recruitment overfishing needs to be addressed.

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