AGE, GROWTH, AND REPRODUCTION OF GAG, MYCTEROPERCA MICROLEPIS (PISCES: SERRANIDAE), IN THE EASTERN GULF OF MEXICO

Peter B. Hood and Rodric A. Schlieder

ABSTRACT

A total of 1,331 gag, Mycteroperca microlepis, captured in the eastern Gulf of Mexico from November 1977 to May 1980 were sampled for life history analysis. Gag captured in waters less than 30 m deep by commercial and nearshore recreational fishermen were significantly smaller ($\overline{TL} \le 739$ mm) than those captured in greater depths ($\overline{TL} \ge 832$ mm). Analyses of marginal increments, annulus spacing, and the relationship of otolith size to fish length suggested that a ring forms on the sagittae once each year during the summer. Growth of gag was greatest during the first 10 years, after which mean size approached an apparent maximum of about 1,100 mm TL. Estimates of the von Bertalanffy growth equation parameters (standard error) for gag were as follows: L_{∞} = 1,190 mm TL (22 mm), K = 0.166 (0.009), and t_0 = -0.62 (0.13). Growth rate estimates determined from monthly length-frequency data for juveniles and from historical tagging data for adults agreed with the estimate determined by analyzing otolith sections. Gag are protogynous hermaphrodites, and females in the sample outnumbered males 6:1. Females became mature between ages III and VI, and no males less than age V were observed. Histological and gravimetric analyses of gonad condition suggested that gag spawn from December to May, with peak activity occurring during February and March.

The gag, Mycteroperca microlepis, is a demersal serranid that ranges from New York to Rio de Janeiro, excluding the West Indies (Briggs, 1958; Smith, 1971). Along the United States Atlantic coast and in the Gulf of Mexico, gag are associated with inshore-reef and shelf-break habitats (Smith et al., 1975; Huntsman, 1976; Huntsman and Dixon, 1976). Along the west coast of Florida, gag are an important part of the grouper/snapper fishery; recent landings of gag by the commercial and recreational fisheries during 1986–1988 have totaled over 2,154,880 kg.¹

Studies conducted in the South Atlantic Bight report that gag are long-lived, slow-growing fish that may live more than 20 years (Collins et al., 1987) and may grow to total lengths measuring over 1,200 mm (Manooch and Haimovici, 1978). McErlean and Smith (1964) proposed that gag are protogynous hermaphrodites based on the remains of the ovarian lumen and lamellae and on the degenerating oocytes in newly transformed males. Furthermore, they observed no females over age X and no males under age XIII. Females in the South Atlantic Bight reach maturity by age V, and no males younger than age V were observed (Collins et al., 1987). In both the South Atlantic Bight and Florida waters, gag spawn from late winter to early spring (McErlean, 1963; Collins et al., 1987).

Concern about the decreasing abundance of grouper stocks in the eastern Gulf of Mexico during the past two decades has prompted research into the life history of these important species. The objective of this paper is to describe the age, growth, and reproduction of gag captured off the coast of west central Florida.

^{&#}x27;Combined landings data from Marine Recreational Fishery Statistics Survey, National Marine Fisheries Service, Silver Springs, Maryland 20910 and Annual Landings Summary, Marine Fisheries Information System, Florida Department of Natural Resources, St. Petersburg, Florida 33701.

MATERIALS AND METHODS

Gag were obtained from the commercial and recreational hook-and-line fisheries based in Pinellas County, Florida, from November 1977 to May 1980. Most of the fish were captured in the eastern Gulf of Mexico between 27°30'N and 28°40'N latitudes at depths ranging from 36 to 180 m. Fish were also collected (using seines, pushnets, hook and line, traps, and spearguns) from nearshore reefs (<15 m deep) west of Tampa Bay and from estuarine locations within Tampa Bay.

Each month, approximately 30 fish representing the entire size range captured were measured (mm TL and mm SL) and weighed (g). Sagittae were removed from the otic capsule and stored in glycerol. Gonads were removed, fixed with Davidson's solution for approximately 24 h, stored in 95% ethanol, and then weighed to the nearest 0.01 g. Length data were stratified at 10-m depth zones and compared using analysis of variance and Tukey's studentized range test for pairwise comparisons (SAS Institute, Inc., 1985). The relationships between SL and TL, and weight with SL and TL were determined by least-squares regression analysis (SAS Institute, Inc., 1985).

Thin sections of sagittae were used for age determination. The left otolith was sectioned through the core at 0.5-mm intervals along a transverse, dorso-ventral plane using a Buehler Isomet low-speed saw with a diamond blade. Mounted sections were placed on a black field, illuminated with reflected light, and examined under a binocular dissecting microscope at 12× magnification. The magnified image of the sectioned otolith was analyzed using a video image analysis system (OPRS; Biosonics, 1987). The number of opaque bands (rings) and the measurements of the distances from the core to the ventral edge of the otolith and from the core to the distal edge of each opaque zone were recorded. Initially, sections from 50 otoliths were read by two investigators to determine the reproducibility of ring counts. The readers agreed on the number of rings in 38 sections (76%). Because only two of the 12 remaining counts differed by more than one ring, one reader examined all otolith sections for age determination. An otolith section was used for age and growth analysis only if two of three separate readings were the same and if the greatest difference between dissimilar readings was only one ring.

Validation of annulus periodicity was determined by analyzing the monthly mean marginal increments and the consistency of the distance from the otolith core to each ring. Monthly mean marginal increments were compared using the Kruskal-Wallis non-parametric analysis of variance (Sokal and Rohlf, 1981), and frequency distributions of sequential ring location within otoliths for each age class were constructed. Monthly mean percent marginal increments [(marginal increment/distance between last two annuli) × 100; Hood et al., in prep.] and monthly mean standardized marginal increments (marginal increment/largest marginal increment recorded for the age class; Collins et al., 1987) were also computed. However, the results of these analyses did not enhance the interpretation of annulus periodicity over monthly mean marginal increments. Therefore, only monthly mean marginal increments are presented here. The relationship between otolith radius and length was determined by least-squares regression analysis (SAS Institute, Inc., 1985).

A gag's length at the time the last annulus was formed was calculated from a regression of total length on otolith radius (Ricker, 1973; Bagenal and Tesch, 1981). Regressions were run on untransformed and log-transformed data, and the regression with the best fit was selected for these calculations. Lengths at the time of last annulus formation were used to estimate the parameters of a von Bertalanffy growth curve using the Marquardt algorithm for calculating a non-linear regression (SAS Institute, Inc., 1985). Seine collections made in Tampa Bay from 1958 to 1981 provided additional length-frequency data for early growth.

To examine the reproductive biology of gag, a portion of each preserved gonad was embedded in paraffin, thin-sectioned at 5.0 μ m, stained with Harris' hematoxylin, and counter-stained with eosin (Humason, 1972). Sections were examined under a compound microscope to determine sex and gonad-development state. We used gonad classes originally devised by Moe (1969) to describe gonad development in the red grouper (*Epinephelus morio*). Gonad classes were examined by age, length, and month. The reproductive state of gag was further examined by calculating a gonosomatic index for each fish (gonad weight•100/whole weight) and comparing monthly means. After sex was determined, we used the Wilcoxon two-sample test (Sokal and Rohlf, 1981) to compare the mean length of females at age to the mean length of males.

RESULTS

A total of 1,331 gag ranging from 17 to 1,222 mm in length² were examined during this study (Fig. 1). Tampa Bay collections included juveniles ranging from 17 to 360 mm in length (Fig. 1A), whereas nearshore collections included both

² Unless stated otherwise, lengths are reported as total length.

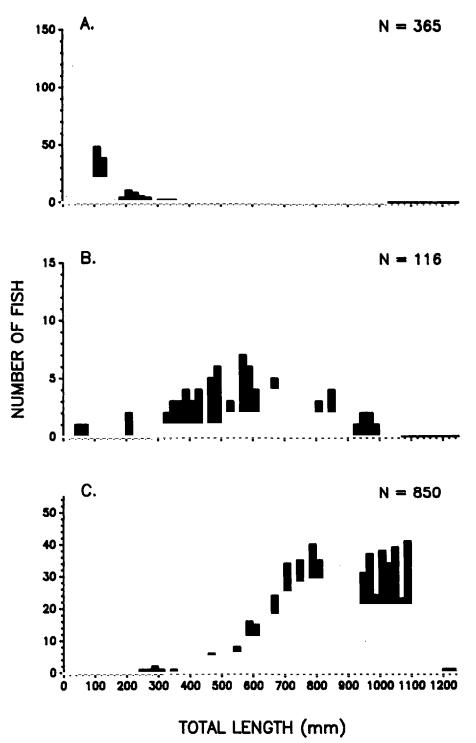


Figure 1. Size distribution of gag collected from the following: A) Tampa Bay by seine; B) nearshore reefs off Tampa Bay by seines, pushnets, hook and line, traps, and speargun; and C) the commercial and recreational hook-and-line catch.

Table 1. Least squares linear regression equations for standard length (SL) on total length (TL), total length on standard length, and whole weight (WT) on total length and on standard length for gag taken from the eastern Gulf of Mexico (N = 802)

Least Squares Equation	p2
SL = 0.870(TL) - 24.741	0.998
TL = 1.147(SL) + 30.299	0.998
$\log_{10}WT = 3.059 (\log_{10}TL) - 5.089$	0.982
$log_{10}WT = 2.958 (log_{10}SL) - 4.569$	0.983

juveniles and adults ranging from 20 to 1,000 mm (Fig. 1B). Lengths of gag collected from the commercial and recreational fisheries ranged from 257 to 1,222 mm (Fig. 1C). Regressions of SL on TL and SL on weight resulting from these data are shown in Table 1.

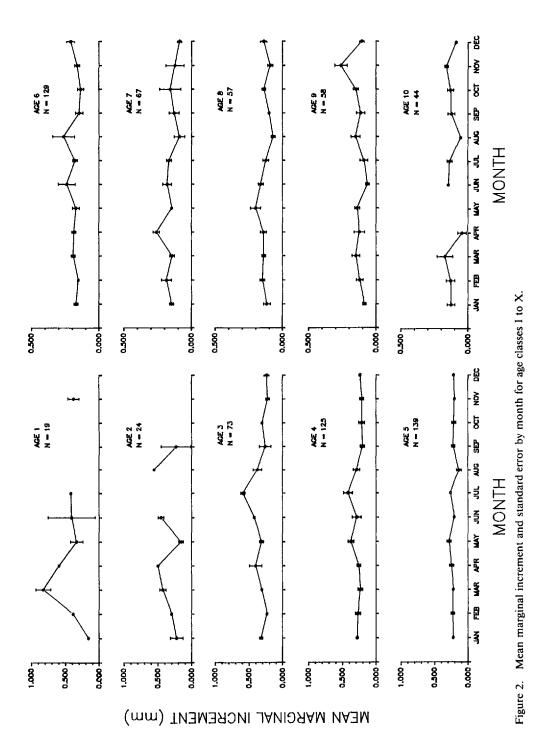
The mean size of gag captured by the commercial and recreational fisheries increased with increasing depth (Anova, P < 0.001). Mean lengths ranged from 499 mm at 10-m depths to 995 mm at 80-m depths (Table 2). Although mean size generally increased from 10- to 80-m depths, pairwise comparisons showed that only gag captured at 10- to 30-m depths were significantly smaller (P < 0.05) than gag captured at greater depths (Table 2).

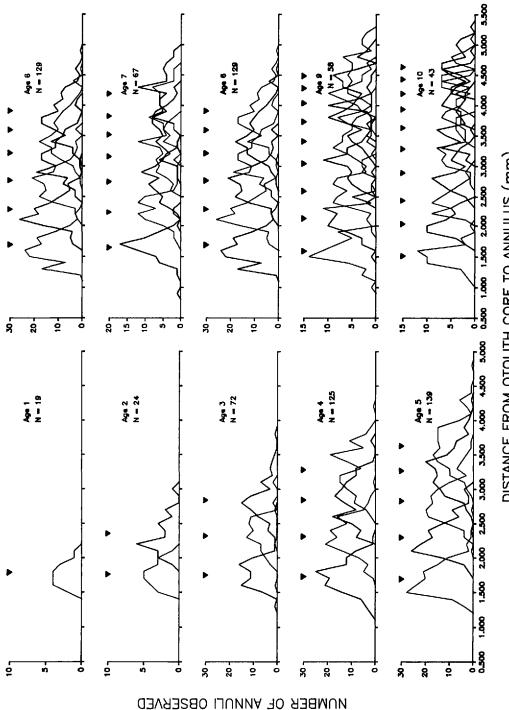
Otoliths were examined from 978 gag ranging from 202 to 1,222 mm in length. The number of opaque bands present in the otoliths ranged from 0–21; however, accurate measurements could only be recorded in otoliths with up to 17 bands. Sixty-five of the otoliths (6.7%) were illegible; and in 111 otoliths (11.4%), bands could be counted but no measurements could be recorded because sections were broken, otoliths were oddly shaped, or cores were missed in the sectioning process. Consequently, age and growth data were derived from only the readable portion of the sample (802 fish; 81.9%). The largest fish examined (1,222 mm) had 17 bands.

Validation of the periodic band deposition was difficult because little variation was observed between monthly mean marginal increments for most age groups (Fig. 2). Of the 10 age groups examined, only gag with three rings (Age III) showed a significant difference between monthly mean marginal increments (Kruskal-Wallis nonparametric analysis of variance, P < 0.01). However, for all classes

Table 2. Mean length (mm), standard error (SE), and number of gag ($N \ge 12$) collected from different depths (m) off west central Florida. A multiple comparison of mean lengths by depth using Tukey's studentized range test yielded three groups (A-C) where mean lengths assigned the same letter are not significantly different from each other

Group						Depth
Ā	В	С	Length	SE	N	(m)
A	В		902	28	12	170
Α	В		828	30	15	110
	В		995	22	32	80
Α	В		895	13	140	70
	В		920	13	152	60
Α	В		876	23	64	50
Α	В		832	14	111	40
Α	В	C	739	21	30	30
Α		С	639	13	104	20
		С	499	23	38	10





DISTANCE FROM OTOLITH CORE TO ANNULUS (mm)

examined except age IX, the widest monthly mean marginal increment was observed between March and August, which suggests that opaque band deposition is completed during this time period.

Periodic band deposition is indirectly supported by 1) the consistency of ring location from the otolith core and 2) the positive correlation of otolith size and fish length. For all age groups, frequency distributions of the distance of each ring from the otolith core was modal, and the location of these modes remained consistent among age classes. For example, the mode for the first ring remains between 1.0 and 2.5 mm, the second between 1.5 and 3.0 mm, the third between 2.0 and 4.0 mm, the fourth between 2.5 and 4.5 mm, etc. (Fig. 3). However, as the number of rings increases, the modes for the fifth ring and above become less defined, possibly due to the increased variability, with time, in otolith growth. The natural log of otolith radius and the natural log of fish length gave the best fit for the regression of length on otolith radius and is described by the following relationship: $ln(TL) = (1.117 \cdot ln \text{ (otolith radius)}) + 5.146 (r^2 = 0.850)$. Despite the inconclusive nature of our validation data, evidence given by other authors (McErlean, 1963; Matheson and Huntsman, 1984; Matheson et al., 1986; and Collins et al., 1987, 1990) leads us to assume that one opaque band is formed each year of life.

Growth rates of gag were greatest through age X, after which mean size approached an apparent maximum of about 1,100 mm (Table 3A). Age and calculated length data from 797 gag were fit to a von Bertalanffy growth curve and were defined by the following parameters (standard error): $L_{\infty}=1,180$ mm (28 mm), K=0.165 (0.013), and $t_{\rm o}=-0.74$ (0.199). The fish selected for these calculations ranged in age from I to XVII and had mean lengths ranging from 422 mm for age I to 1,140 mm for age XVII. Analysis of monthly length-frequency data from gag captured in Tampa Bay showed that gag can grow to 220–340 mm by the end of their first year. Juvenile gag were 17–40 mm long in April, and by the following February they were 220–340 mm long (Fig. 4). The length at age I predicted by the von Bertalanffy growth curve (281 mm; Table 3A) falls within this range.

Overall, female gag outnumbered males by approximately 6:1 (818:134), and six transitional gag were observed. However, the percentage of females decreased as size and age increased (Table 4). Fish were exclusively female at sizes less than 812 mm and ages less than V; however, by 1,050 mm and age XI, males comprised about 50% of the sample. Between ages V and XI, mean lengths of males were greater than those of females; however, only at ages VIII and X were males significantly larger (P < 0.05, Table 3). After age XI, mean sizes at age for males and females were not significantly different.

Females reach maturity primarily between ages III and IV, and their transformation into males begins as early as age V. Mature females were observed at ages II–XVI (Table 4). By age IV, 70% of females were mature (classified as either mature resting, mature active, or spent), and 100% were mature by age VI. Gonads from 12 aged individuals were transforming into testes or had just transformed (immature males). These individuals ranged from age V to XIII; five of the 12 were ages VIII or IX.

Figure 3. Frequency distributions of the distance from the otolith core to each band for age classes I to X. Inverted triangles indicate mean location of each band.

Table 3. Number of gag sampled, mean length, (standard error), and minimum and maximum lengths for ages 0–XXI presented for (A) Sexes combined, (B) Females, and (C) Males. Predicted length is based on the von Bertalanffy growth curve $TL = 1,180 \cdot [1 - e^{-0.165 \cdot (1 + 0.74)}]$. * = Mean length of females significantly different from males of the same age

Age	N	Observed Mean TL (SE)	Min TL	Max TL	Predicted TL
A. Sexes Combin	ed				
0	5	322 (16)	283	361	
I	19	383 (17)	257	530	281
II	24	476 (15)	350	678	420
III	78	592 (9)	443	785	538
IV	126	695 (8)	487	910	637
V	143	779 (7)	467	992	722
VI	138	828 (8)	654	1,110	793
VII	79	896 (8)	676	1,041	854
VIII	63	942 (9)	802	1,067	905
IX	69	981 (7)	765	1,085	949
X	48	1,024 (10)	890	1,129	986
ΧI	30	1,043 (18)	642	1,170	1,017
XII	13	1,079 (9)	1,030	1,125	1,044
XIII	18	1,079 (6)	1,029	1,123	1,066
XIV	13	1,092 (15)	1,010	1,222	1,085
XV	9	1,088 (15)	1,008	1,127	1,101
XVI	6	1,091 (20)	1,035	1,165	1,115
XVII	3	1,089 (2)	1,086	1,089	1,126
XVIII	1	1,130 (—)	-	_	1,136
XIX	0	_	_	_	1,144
XX	2	1,060 (21)	1,039	1,080	1,151
XXI	1	1,140 (-)	_	_	1,157
. Females					
0	5	322 (16)	283	361	
I	19	383 (17)	257	530	
II	24	476 (15)	350	678	
III	78	593 (9)	443	785	
IV	126	695 (8)	487	910	
V	141	778 (7)	467	980	
VI	135	824 (7)	654	1,020	
VII	77	896 (9)	676	1,040	
VIII	59	937* (9)	802	1,065	
IX	56	976 (8)	765	1,085	
X	27	989* (13)	890	1,085	
ΧI	16	1,023 (31)	642	1,170	
XII	3	1,096 (7)	1,085	1,110	
XIII	5	1,054 (12)	1,029	1,100	
XIV	3	1,110 (20)	1,082	1,150	
XV	2	1,086 (38)	1,048	1,124	
XVI	2	1,081 (47)	1,035	1,128	
XVII	0	-		_	
XVIII	0		_	_	
XIX	0	_	_	_	
XX	0	_	_	_	
XXI	0	_	_	_	
. Males					
0	1	992 (-)	_	_	
Ĭ	2	1,085 (25)	1,060	1,110	
II	1	946 (–)	1,000	1,110	
III	4	1,019 (22)	971	1,067	
IV	13	1,002 (17)	865		
				1,085	
V	21	1,070 (7)	1,018	1,129	
VI	14	1,068 (13)	998	1,150	

Table 3. Continued

Age	N	Observed Mean TL (SE)	Min TL	Max TL	Predicted TL
VII	9	1,075 (12)	1,030	1,125	
VIII	12	1,089 (6)	1,050	1,123	
IX	10	1,088 (18)	1,010	1,222	
X	7	1,088 (17)	1,008	1,127	
ΧI	4	1,096 (24)	1,059	1,165	
XII	3	1,089 (2)	1,086	1,094	
XIII	1	1,130 (-)	·	_	
XIV	0	– ` ´	_	_	
χV	2	1,059 (21)	1,039	1,080	
XVI	1	1,140 ()	´ —	· -	
XVII	0	– ` ´	_	_	
XVIII	0	_		_	
XIX	Ö	_	_	_	
XX	Õ	_	_	_	
XXI	0	_	_	_	

Gag have a protracted spawning period that extends at least from December to May. Spent females were observed during this period (Fig. 5A). The high percentage of mature active and spent females in February and March indicated that peak spawning occurred at this time. Gag with ripe and spent testes were most prevalent from November to May (Fig. 5B). Little spawning, if any, occurred during the summer and fall months and was evidenced by a high percentage of females with mature resting ovaries from June through November and a high percentage of males with mature inactive testes from June to October.

These observations of a winter-spring period of active spawning and a summerfall period of inactivity were also apparent in trends of monthly mean gonosomatic indices and collections of juvenile gag. For both males and females, the relative weight of gonads increased from September to March, indicating ripening (Fig. 6). Relative weight decreased from March to September, indicating that gametes shed and that the gonads entered the spent-resting state. For females, dramatic increases in relative gonad weight in February and March (1.31 and 1.83, respectively) indicated peak spawning. Winter and spring spawning were also indicated by the presence of small juveniles that were captured with seines during April (17–36 mm) and May (18–71 mm) in Tampa Bay (Fig. 4). Estimated ages of similar-sized fish from South Carolina are 40–60 and 40–80 days old, respectively (Keener et al., 1988).

DISCUSSION

The mean sizes of gag captured in the eastern Gulf of Mexico by the commercial and recreational hook-and-line fisheries increased as the depth of capture increased, up to a depth of 80 m. This increase in size with depth has also been reported for gag by Moe (1966, 1972), Huntsman and Dixon (1976), and Manooch and Haimovici (1978) and may indicate that different fishing pressures have been exerted at different depths and thus that larger fish have been previously removed, or it may indicate that gag migrate to deeper waters as they mature. Keener et al. (1988) reported that although young-of-the-year gag occur in high-salinity barrier island inlets in South Carolina, they are virtually absent in offshore trap collections. Juvenile gag were also found in the estuarine waters of Tampa Bay, where McErlean

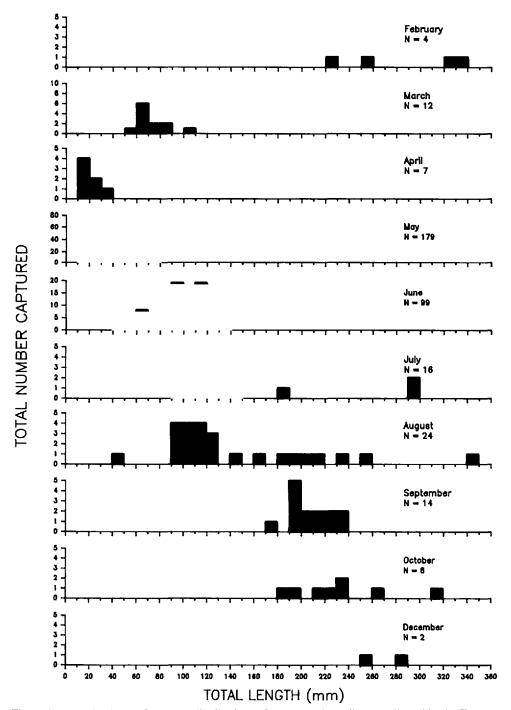


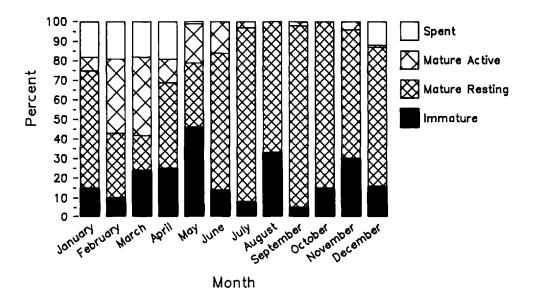
Figure 4. Monthly length-frequency distributions of larval and juvenile gag collected in the Tampa Bay estuary from June 1958 to June 1981.

Table 4. Number and percentage of gag by stage of sexual maturity for A) total length (TL) and B) age. IMF = immature female, MF = mature female (mature resting, mature active, spent), %MF = percentage of mature females for females combined, T = transitional, IMM = immature males, MM = mature males (mature inactive, ripening mature, ripe, spent), and %F = overall percentage of females. Transitional fish were not used to calculate either %MF or %F

TL Midpoint	IMF	MF	%MF	т.	IMM	мм	%F
			A				
350	6	0	0	0	0	0	100
400	10	0	0	0	0	0	100
450	14	2	13	0	0	0	100
500	19	5	21	0	0	0	100
550	21	6	22	0	0	0	100
600	29	21	42	0	0	0	100
650	16	29	64	0	0	0	100
700	17	59	78	0	0	0	100
750	20	69	78	0	0	0	100
800	7	86	92	ī	Ö	ŏ	100
850	Ö	87	100	Ō	ĭ	Ö	99
900	ŏ	98	100	Ĭ	ō	ŏ	100
950	Ö	76	100	Ô	ĭ	4	94
1,000	Ŏ	64	100	2	4	15	77
1,050	ŏ	37	100	ĩ	3	39	47
1,100	ŏ	15	100	i	ŏ	54	22
1,150	ŏ	5	100	Ô	ŏ	10	33
1,200	ŏ	ŏ	0	ŏ	ŏ	3	ő
Age	IMF	MF	%MF	T	IMM	мм	%F
· · · · · · · · · · · · · · · · · · ·			В				
I	16	0	0	0	0	0	100
ĪI	20	i	5	Õ	ŏ	Ö	100
ĪĪI	52	25	32	Ö	ŏ	ŏ	100
ΪV	38	88	70	ŏ	ŏ	ŏ	100
v	22	118	84	ī	Ö	ĺ	99
VI	6	129	96	i	i	ī	98
VII	ŏ	77	100	i	Ö	1	99
VIII	ŏ	59	100	Ö	2	2	94
IX	0	56	100	Ŏ	3	10	81
X	Ō	28	100	Ō	1	20	57
ΧI	Ö	16	100	Ŏ	0	14	53
XII	ŏ	3	100	ĭ	ŏ	9	25
XIII	ŏ	5	100	î	ŏ	13	28
XIV	ő	3	100	ò	0	10	23
XV	ő	2	100	ő	Ö	7	22
XVI	Ö	2	100	Ö	0	4	33
XVII	0	0	-	0	0	3	0
XVIII	0	0	_	0	0	1	0
XIX	0	0		0	0	0	_
XX	0	0		ő	0	2	0
XXI	0	0	_	0	0	1	0
ЛЛІ	U	U		U	U	1	U

(1963) reported them abundant in the bycatch of the bait shrimp fishery. This observation led Moe (1966) to suggest that juvenile gag may migrate offshore from estuarine areas. Tagging studies indicate that adult gag show "residence specificity" to reefs (Moe, 1966; Beaumariage, 1969); therefore, after juveniles leave estuarine waters for deeper waters, they become site specific. The degree of this site specificity is unknown. Collins et al. (1990) tagged several large gag (≥75 cm TL) that traveled from reefs off Charleston, S.C., to southern Florida. They

A. Female



B. Male

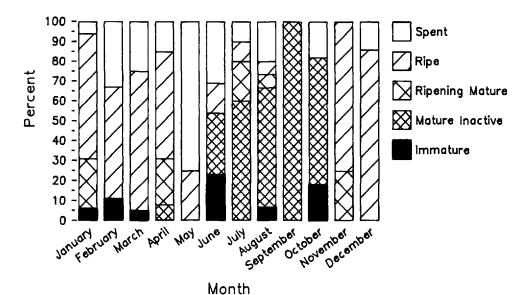


Figure 5. Percent frequency of reproductive classes each month for A) females and B) males.

hypothesized that at least some gag in the South Atlantic Bight may undergo a spawning migration to south Florida. Whether these gag return to their original point of departure or if northeastern Gulf of Mexico gag undergo a similar migration is unknown.

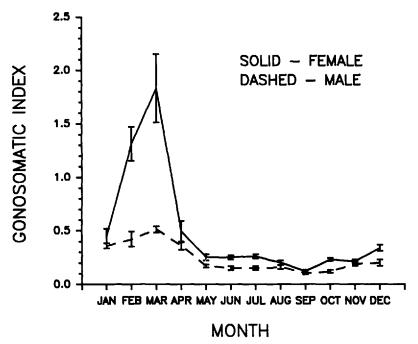


Figure 6. Mean gonosomatic index (±1 SE) plotted at monthly intervals for male and female gag.

Sagittae could readily be used to determine the age of gag. Approximately 95% of otolith sections were legible for determining age. This compares favorably with other studies that also used otoliths to age gag (Manooch and Haimovici, 1978 [79%]; Collins et al., 1987 [87%]). Marginal increment data suggest that opaque band formation occurs during the spring and summer in the eastern Gulf. McErlean (1963) examined whole otoliths from gag captured off the west coast of Florida and found annuli formed from April to July. Analysis of sectioned otoliths from gag captured in the South Atlantic Bight showed that annuli were laid down in the late spring and midsummer for gag less than age IX and in August for gag greater than age VIII (Collins et al., 1987). The regular position of corresponding bands is further evidence that the bands are deposited once a year. Similar analyses of these types of data have been used for the validation of annuli periodicity in scamp (M. phenax; Matheson et al., 1986), speckled hind (Epinephelus drummondhayi), and snowy grouper (E. niveatus; Matheson and Huntsman, 1984). Direct evidence for yearly deposition of annuli in gag was demonstrated by Collins et al. (1990) using tetracycline-injected, tagged fish. However, a true validation of band periodicity as suggested by Beamish and McFarlane (1983) for Gulf of Mexico gag is still needed.

The maximum observed age of gag in the eastern Gulf (21 years) is similar to that observed for gag in the South Atlantic Bight (22 years; Collins et al., 1987). These maximum ages are much greater than those observed by McErlean (1963) in the eastern Gulf and by Manooch and Haimovici (1978) in the South Atlantic Bight. These authors examined whole otoliths and counted a maximum of 13 annuli. Our data support the contention made by Collins et al. (1987) that annuli at the edge of gag otoliths are more readily observed in otolith sections than they are in whole otoliths.

Our estimates of growth yielded lengths at age which were larger than that of McErlean (1963) for this species along the west central Florida coast. Our predicted

Table 5. Actual growth of tagged gag, Mycteroperca microlepis, compared to growth estimated from
a von Bertalanffy growth curve. Age at first capture is predicted from the curve. Data are from Topp
(1963), ^a Beaumariage (1964), ^b Beaumariage and Wittich (1966), ^c Beaumariage (1969), ^d and Moe (1970)

First capture			Grand	th (mm)	
Predicted age (yrs)*	Length (mm) Days at large		Actual (A)	Predicted (P)	Difference (A - P)
1.90	328°	814	155	321	-166
2.14	364ª	634	223	261	-38
2.56	425 ^d	815	155	280	-125
2.70	445°	337	105	157	-51
2.73	449 ^d	322	51	151	-101
2.84	464ª	704	204	240	-36
3.96	600⁴	423	90	131	-41
7.40	890₫	1,130	162	111	+50
1.83	317ь	488	161	238	-77
2.18	371 ^b	378	68	190	-122
1.84	320b	362	110	200	-90
4.62	670°	2,307	381	346	+35
1.34	238ª	207	34	171	-136
1.69	295ª	140	10	134	-124

^{*} Predicted age was calculated by estimating the von Bertalanffy growth parameters using the Marquardt algorithm for calculating a non-linear regression on the same data (SAS Institute, Inc., 1985) but solving the von Bertalanffy growth equation for age instead of length. This calculation yielded the following parameters (standard error): $L_x = 1,267$ mm TL (37 mm), K = 0.166 (0.0001), and $T_0 = 0.10$ (0.0001).

lengths at age ranged from 295 mm at age I to 793 mm at age VI, whereas those of McErlean (1963) ranged from 210 mm (191 mm SL) at age I to 720 mm (590 mm SL) at age VI. The reason for this discrepancy is unknown; however, our observed empirical growth rate (Table 3A) was very close to that reported by Collins et al. (1987) for gag from the South Atlantic Bight: 347 mm for age I, 824 mm for age VI, and 1,125 mm for age XXI. Growth data from tagging studies in the eastern Gulf showed a slower growth rate than that estimated in our study. Using length data for 15 fish from studies by Topp (1963), Beaumariage (1964, 1969), Beaumariage and Wittich (1966), and Moe (1970), actual growth was compared to predicted growth employing the von Bertalanffy growth curve calculated in this study (Table 5). Our curve generally over-estimated the observed growth of 13 of 15 tagged fish.

Our estimates of growth-curve parameters are the only estimates available for gag in the eastern Gulf of Mexico. Comparing von Bertalanffy growth parameters calculated by Manooch and Haimovici (1978) for gag captured in the South Atlantic Bight ($L_{\infty}=1,290$ mm TL, K=0.12154 and $t_{o}=-1.127$) to these parameters calculated in our study, predicted sizes at age would be 1) similar at age I, 2) smaller in the southeast Atlantic at ages II–XII, and 3) larger in the southeast Atlantic at ages above XII. Our estimated parameters are within the ranges for serranids given by Manooch (1987); i.e., a maximum age over 10 years and K between 0.10 and 0.25.

The overall sex ratio of fish collected in the eastern Gulf was overwhelmingly female, with a low incidence of fish in transition. McErlean and Smith (1964) examined histological preparations of 32 gag gonads, and females outnumbered males by 15:1. Collins et al. (1987) also examined gag gonads histologically and found an overall sex ratio of about 6:1. We observed few transitional gonads in our study (1.1%). Collins et al. (1987) also found a low percentage (1.25%) and hypothesized that sexual transformation occurs rapidly; i.e., few individuals are found in this stage. Roberts and Schlieder (1983) artificially induced sexual trans-

formation in gag using orally administered testosterone and found gonad reversal to occur within 150 days.

Female gag mature as early as ages II-III in the eastern Gulf of Mexico, which is similar to the observed age at maturity for gag in the South Atlantic Bight (Collins et al., 1987). McErlean and Smith (1964) estimated that gag females mature around their fifth or sixth year; however, they looked at only 32 gag, only four of which were age IV and none of which were age III. McErlean and Smith (1964) estimated that females transform to males during their tenth or eleventh year. We and Collins et al. (1987) found that sexual transformation can occur as early as age V, and we observed the highest frequency of transforming individuals between ages VIII and IX.

The mean size of females from ages V to IX was less than that observed for males. This difference suggests that at these ages, the largest females transform to males or that once sexual transformation is complete, the rate of growth increases rapidly. Because the sizes of males and females are comparable at ages greater than X, the first interpretation appears more likely.

Gag spawn from November to May, with peak activity occurring in February and March in the eastern Gulf. McErlean (1963) also found that gag sampled off west central Florida spawned during the winter and spring, with peak spawning activity occurring from January to March. Peak spawning of gag from the South Atlantic Bight occurs later in the year, from late March to early April (Collins et al., 1987; Keener et al., 1988).

Gag fit the generalized model for serranid growth and reproduction: they are long-lived, slow-growing, protogynous hermaphrodites (Manooch, 1987; Shapiro, 1987). Manooch and Haimovici (1978) warn that the gag may be susceptible to over-harvesting because it grows slowly, is a top-level carnivore, and is habitat-specific. Furthermore, protogynous hermaphroditism results in an unequal sex ratio in which there are fewer, older, and larger males. This inequality may result in differential fishing mortality for the two sexes (Shapiro, 1987). These factors need to be considered when developing management strategies for this species.

ACKNOWLEDGMENTS

We thank M. F. Godcharles and L. H. Bullock for assistance in the field; K. J. Peters and M. M. Leiby for use of their larval and juvenile gag data; J. E. Williams for histological preparations; E. McManus for his diligence at the otolith saw; and J. J. Kimmel, J. Leiby, B. Mahmoudi, R. E. Matheson, M. D. Murphy, K. J. Peters, R. G. Taylor, and two anonymous reviewers for their help in reviewing this paper. This study was funded in part by the U.S. Department of Commerce, National Oceanographic Atmospheric Administration, National Marine Fisheries Service under PL 88-309 Project No. 2-341-R and PL 99-659, Project 2-IJ-2.

LITERATURE CITED

- Bagenal, T. B. and F. W. Tesch. 1981. Age and growth. Pages 101-136 in T. B. Bagenal, ed. Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford.
- Beamish, R. J. and G. A. McFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112: 735-743.
- Beaumariage, D. S. 1964. Returns from the 1963 Schlitz tagging program. Fla. Bd. Conserv. Mar. Lab. Tech. Ser. No. 43. 34 pp.
- ——. 1969. Returns from the 1965 Schlitz tagging program including a cumulative analysis of previous results, Fla. Bd. Conserv. Mar. Lab. Tech. Ser. No. 59. 38 pp.
- —— and A. C. Wittich. 1966. Returns from the 1964 Schlitz tagging program. Fla. Bd. Conserv. Mar. Lab. Tech. Ser. No. 47. 50 pp.
- Biosonics. 1987. Optical pattern recognition system. Biosonics, Inc., Seattle, Washington. 139 pp. Briggs, J. C. 1958. A list of Florida fishes and their distribution. Bull. Fla. State Mus. Biol. Ser. 2: 223-318.

- Collins, M. R., S. B. Van Sant and D. J. Schmidt. 1990. Age validation of tag-recaptured reef fish off South Carolina. Page 73 in 70th Annual Meeting of the American Society of Ichthyologists and Herpetologists. (Abstract.)
- ——, C. W. Waltz, W. A. Roumillat and D. L. Stubbs. 1987. Contribution to the life history and reproductive biology of gag, *Mycteroperca microlepis* (Serranidae), in the South Atlantic Bight. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 85: 648-653.
- Humason, G. L. 1972. Animal tissue technique. W. H. Freeman & Co., San Francisco, California. 641 pp.
- Huntsman, G. R. 1976. Offshore headboat fishing in North and South Carolina. U.S. Natl. Mar. Fish. Serv. Mar. Fish. Rev. 33: 13-23.
- —— and R. L. Dixon. 1976. Recreational catches of four species of groupers in the Carolina headboat fishery. Proc. 29th Annual Conf. S.E. Assoc. Game Fish Comm. 29: 185–194.
- Keener, P., G. D. Johnson, B. W. Stender, E. B. Brothers and H. R. Beatty. 1988. Ingress of postlarval gag, *Mycteroperca microlepis* (Pisces: Serranidae), through a South Carolina barrier island inlet. Bull. Mar. Sci. 42: 376-396.
- Manooch, C. S. 1987. Age and growth of snappers and groupers. Pages 329-373 in J. J. Polovina and S. Ralston, eds. Tropical snappers and groupers; biology and fisheries management. Westview Press, Inc., Boulder and London.
- and M. Haimovici. 1978. Age and growth of the gag *Mycteroperca microlepis* and size-age composition of the recreational catch off the southeastern United States. Trans. Am. Fish. Soc. 107: 234–240.
- Matheson, R. H. and G. R. Huntsman. 1984. Growth, mortality, and yield-per-recruit models for the speckled hind and snowy-grouper from the United States South Atlantic Bight. Trans. Am. Fish. Soc. 113: 607-616.
- -, and C. S. Manooch. 1986. Age, growth, mortality, food and reproduction of the scamp, *Mycteroperca phenax*, collected off North Carolina and South Carolina. Bull. Mar. Sci. 38: 300-312.
- McErlean, A. J. 1963. A study of the age and growth of the gag, *Mycteroperca microlepis* Goode and Bean (Pisces: Serranidae), on the west coast of Florida. Fla. Bd. Conserv. Mar. Lab. Tech Ser. No. 41. 29 pp.
- —— and C. L. Smith. 1964. The age of sexual succession in the protogynous hermaphrodite *Mycteroperca microlepis*. Trans. Am. Fish. Soc. 93: 301–302.
- Moe, M. A. 1966. Tagging fishes in Florida offshore waters. Fla. Bd. Conserv. Mar. Lab. Tech. Ser. No. 49, 40 pp.
- 1969. Biology of the red grouper Epinephelus morio (Valenciennes) from the eastern Gulf of Mexico. Fla. Dep. Nat. Resour. Mar. Res. Lab. Prof. Pap. Ser. 10. 95 pp.
- ——. 1970. Return of tagged gag, *Mycteroperca microlepis*, and Caribbean red snapper, *Lutjanus campechanus*, after six years of freedom. Trans. Am. Fish. Soc. 99: 428–429.
- ——. 1972. Movement and migration of south Florida fishes. Fla. Bd. Conserv. Mar. Lab. Tech. Ser. No. 69. 25 pp.
- Ricker, W. E. 1973. Linear regressions in fishery research. J. Fish. Res. Bd. Can. 30: 409-434.
- Roberts, D. E. and R. A. Schlieder. 1983. Induced sex inversion, maturation, spawning and embryogeny of the protogynous grouper, *Mycteroperca microlepis*. J. World Maricult. Soc. 14: 639–649.
- SAS Institute, Inc. 1985. SAS user's guide: statistics. SAS Institute, Inc., Cary, North Carolina. 956 pp.
- Shapiro, D. Y. 1987. Reproduction in groupers. Pages 295-327 in J. J. Polovina and S. Ralston, eds. Tropical snappers and groupers: biology and fisheries management. Westview Press, Inc., Boulder and London.
- Smith, C. L. 1971. A revision of the American grouper *Epinephelus* and allied genera. Bull. Am. Mus. Nat. Hist. 146: 71-241.
- Smith, G. B., H. M. Austin, S. A. Bortone, R. W. Hastings and L. H. Ogren. 1975. Fishes of the Florida Middle Grounds with comments on ecology and zoogeography. Fla. Mar. Res. Publ. No. 9. 14 pp.
- Sokal, R. R. and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Co., New York. 859 pp.
- Topp, R. 1963. The tagging of fishes in Florida 1962 program. Fla. State Bd. Conserv. Prof. Pap. Ser. No. 5. 76 pp.

DATE ACCEPTED: December 10, 1991.

Address: Florida Marine Research Institute, Department of Natural Resources, 100 Eighth Avenue S.E., St. Petersburg, Florida 33701-5095.

A. Sexes Combined

significantly different from males of the same age

N

Min TL

Max TL

Predicted TL

Table 3. Number of gag sampled, mean length, (standard error), and minimum and maximum lengths for ages 0-XXI presented for (A) Sexes combined, (B) Females, and (C) Males. Predicted length is based on the von Bertalanffy growth curve $TL = 1,180 \cdot [1 - e^{-0.165 \cdot (t + 0.74)}]$. $\stackrel{\bullet}{=}$ Mean length of females

Observed Mean TL (SE)

ERRATUM

Age, Growth, and Reproduction of Gag Mycteroperca microlepis (Pisces: Serranidae), in the Eastern Gulf of Mexico.

Peter B. Hood and Rodric A. Schlieder

Bulletin of Marine Science 51(3): 337-352

e, PLEASE REFER TO THIS CORRECTED VERSION OF TABLE THE TEXT IS INCORRECT. Z ~ TABLE

	ı		
1	١		
1			
1	١		
THE REPORT OF THE PROPERTY OF			
2			
1001			
i			
)			

0 5 322 (16) 283 361 I 1 9 383 (17) 257 530 281 III 24 476 (15) 350 678 420 IIII 78 592 (9) 443 785 538 IV 126 695 (8) 487 910 637 V 1 138 828 (8) 654 1,110 793 VII 179 896 (8) 676 1,041 854 VIII 63 942 (9) 802 1,067 905 IX 69 981 (7) 765 1,085 949 X 48 1,024 (10) 890 1,129 986 X 1 30 1,043 (18) 642 1,170 1,017 XIII 13 1,079 (9) 1,030 1,125 1,044 XIV 13 1,092 (15) 1,010 1,222 1,085 XV 9 1,088 (15) 1,008 1,127 1,101 XVII 3 1,092 (15) 1,010 1,222 1,085 XV 9 1,088 (15) 1,008 1,127 1,101 XVII 1 1,130 (-) 1,136 XXX 0 1,136 XXX 2 1,066 (21) 1,039 1,080 1,151 XXX 1 1 1,140 (-) 1,157 B. Females 0 5 322 (16) 283 361 II 24 476 (15) 350 678 III 25 476 (15) 350 678 III 24 476 (15) 350 678 III 25 476 (15) 350 678 III 27 1,000 (10) IX 58 (10) 654 1,020 IX 135 824 (7) 654 1,020 IX 14 6 1,023 (31) 642 1,170 IX 135 824 (7) 654 1,020 IX 14 6 1,023 (31) 642 1,170 IX 15 6 976 (8) 765 1,085 IX 1 16 1,023 (31) 642 1,170 IX 11 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	^	. Sexes Combine	a					
III		0	5	322 (16)	283	361		
III		I	19	383 (17)	257	530	281	
IV		II .	24	476 (15)	350		420	
VI 138 828 (8) 654 1,110 793 VII 79 896 (8) 676 1,041 854 VIII 63 942 (9) 802 1,067 905 IX 69 981 (7) 765 1,085 949 X 48 1,024 (10) 890 1,129 986 XI 30 1,043 (18) 642 1,170 1,017 XIII 13 1,079 (9) 1,030 1,125 1,044 XIII 18 1,079 (6) 1,029 1,123 1,066 XIV 13 1,092 (15) 1,010 1,222 1,085 XV 9 1,088 (15) 1,008 1,127 1,101 XVI 6 1,091 (20) 1,035 1,165 1,115 XVIII 3 1,089 (2) 1,086 1,089 1,126 XVIII 1 1,130 (-) 1,136 XXX 2 2 1,060 (21) 1,035 1,165 1,115 XXXI 1 1,140 (-) 1,136 XXX 1 1 1,140 (-) 1,136 B. Females 0 5 322 (16) 283 361 I 24 476 (15) 350 678 III 778 593 (9) 443 785 IV 126 695 (8) 487 910 V 141 778 (7) 467 980 VI 177 896 (9) 676 1,040 VIII 77 896 (9) 676 1,040 VIII 77 896 (9) 676 1,040 VIII 59 937* (9) 802 1,065 IX 56 976 (8) 765 1,085 X 27 989* (13) 890 1,085 X 27 989* (13) 890 1,085 X 1 16 1,023 (31) 642 1,170 XIII 3 1,096 (7) 1,085 1,110 XIII 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0		III	78	592 (9)	443	785	538	
V		IV	126	695 (8)	487	910	637	
VII 79 896 (8) 676 1,041 854 VIII 63 942 (9) 802 1,067 905 IX 69 981 (7) 765 1,085 949 X 48 1,024 (10) 890 1,129 986 XI 30 1,043 (18) 642 1,170 1,017 XII 13 1,079 (9) 1,030 1,125 1,044 XIII 18 1,079 (6) 1,029 1,123 1,066 XIV 13 1,092 (15) 1,010 1,222 1,085 XV 9 1,088 (15) 1,008 1,127 1,101 XVI 6 1,091 (20) 1,035 1,165 XVI 1 3 1,089 (2) 1,086 1,089 1,126 XVIII 1 1,130 (-) 1,136 XXX 2 2 1,066 (21) 1,039 1,080 1,151 XXX 1 1 1,140 (-) 1,157 B. Females 0 5 322 (16) 283 361 I 19 383 (17) 257 5300 III 24 476 (15) 350 678 III 78 593 (9) 443 785 IV 126 695 (8) 487 910 V 141 778 (7) 467 980 V 141 778 (7) 467 980 V 141 778 (7) 654 1,020 V 141 778 (7) 654 1,020 V 111 59 937* (9) 802 1,065 IX 56 976 (8) 765 1,085 X 27 989* (13) 890 1,085 X 1 16 1,023 (31) 642 1,170 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,106 (20) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,106 (20) 1,085 X 1 1 1,000 1,000 1,000 1,000 XIV 3 1,110 (20) 1,085 X 1 1 1 1,000 1,000 1,000 1,000 XIV 3 1,110 (20) 1,082 1,150 XVI 2 1,081 (47) 1,035 1,128 XVII 0 C. Males 0 0 0 II 0 III 0		V		779 (7)	467	992	722	
VIII 79 896 (8) 676 1,041 854 VIII 63 942 (9) 802 1,067 905 IX 69 981 (7) 765 1,085 949 X 48 1,024 (10) 890 1,129 986 XI 30 1,043 (18) 642 1,170 1,017 XII 13 1,079 (9) 1,030 1,125 1,044 XIII 18 1,079 (6) 1,029 1,123 1,066 XIV 13 1,092 (15) 1,010 1,222 1,085 XV 9 1,088 (15) 1,008 1,127 1,101 XVII 6 1,091 (20) 1,035 1,165 XVII 3 1,089 (2) 1,086 1,089 1,126 XVIII 1 1,130 (-) 1,136 XIX 0 1,144 XX 2 2 1,060 (21) 1,039 1,080 1,151 XXII 1 1,140 (-) 1,157 B. Females 0 5 322 (16) 283 361 I 19 383 (17) 257 530 III 24 476 (15) 350 678 III 78 593 (9) 443 785 IV 126 695 (8) 443 785 IV 126 695 (8) 443 785 IV 126 695 (8) 443 785 IV 127 1,101 XI 178 (7) 467 980 V 141 778 (7) 467 980 V 141 778 (7) 654 1,020 VIII 77 896 (9) 676 1,040 VIII 59 937* (9) 802 1,065 IX 56 976 (8) 765 1,085 X 27 989* (13) 890 1,085 XI 16 1,023 (31) 642 1,170 XIII 3 1,096 (7) 1,085 XI 16 1,023 (31) 642 1,170 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XVI 2 1,081 (47) 1,035 1,128 XVI 2 1,081 (47) 1,035 1,128 XVII 0 C. Males 0 0 0 II 0 III 0		VI	138	828 (8)	654	1,110	793	
IX		VII	79	896 (8)	676	1,041	854	
X 48 1,024 (10) 890 1,129 986 XI 30 1,043 (18) 642 1,170 1,017 XIII 13 1,079 (9) 1,030 1,125 1,044 XIII 18 1,079 (6) 1,029 1,123 1,066 XIV 13 1,092 (15) 1,010 1,222 1,085 XV 9 1,088 (15) 1,008 1,127 1,101 XVI 6 1,091 (20) 1,035 1,165 1,115 XVIII 1 1,130 (-) 1,136 XIX 0 1,136 XIX 0 1,136 XIX 0 1 1,130 (-) 1,136 XIX 0 1 1,140 (-) 1,157 B. Females 0 5 322 (16) 283 361 I 19 383 (17) 257 530 II 24 476 (15) 350 678 III 78 593 (9) 443 785 IV 126 695 (8) 487 910 V 141 778 (7) 467 980 V 111 59 937* (9) 802 1,065 IX 56 976 (8) 80 (9) 676 1,040 VIII 59 937* (9) 802 1,065 IX 56 976 (8) 765 1,085 X 27 989* (13) 890 1,085 X 27 989* (13) 890 1,085 X 11 16 1,023 (31) 642 1,170 XIII 3 1,096 (7) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVI 0		VIII	63	942 (9)	802	1,067	905	
XI		IX	69	981 (7)	765	1,085	949	
XII 13 1.079 (9) 1.030 1.125 1.044 XIII 18 1.079 (6) 1.029 1.123 1.066 XIV 13 1.092 (15) 1.010 1.222 1.085 XV 9 1.088 (15) 1.008 1.127 1.101 XVI 6 1.091 (20) 1.035 1.165 1.115 XVII 1 1.130 (-) 1.136 XXIX 0 1.144 XXX 2 1.060 (21) 1.039 1.080 1.151 XXII 1 1.140 (-) 1.157 B. Females 0 5 322 (16) 283 361 I 19 383 (17) 257 530 II 24 476 (15) 350 678 III 78 593 (9) 443 785 IV 126 695 (8) 487 910 V 141 778 (7) 467 980 VI 135 824 (7) 654 1.020 VII 77 896 (9) 676 1.040 VII 77 896 (9) 676 1.040 VIII 59 937*(9) 802 1.065 IX 56 976 (8) 765 1.085 X 27 989*(13) 890 1.085 X 27 989*(13) 890 1.085 X 11 6 1.023 (31) 642 1.170 XIII 3 1.096 (7) 1.085 1.110 XIII 5 1.054 (12) 1.029 1.100 XIV 3 1.110 (20) 1.082 1.150 XVI 2 1.086 (38) 1.048 1.124 XVII 0		X	48	1,024 (10)	890	1,129	986	
XIII		XI	30	1,043 (18)	642	1,170	1,017	
XIV 13 1,092 (15) 1,010 1,222 1,085 XV 9 1,088 (15) 1,008 1,127 1,101 XVII 6 1,091 (20) 1,035 1,165 1,115 XVIII 3 1,089 (2) 1,086 1,089 1,126 XVIII 1 1,130 (-) — — — 1,136 XIX 0 — — — — 1,144 XX 2 2 1,060 (21) 1,039 1,080 1,151 XXII 1 1,140 (-) — — — 1,151 XXII 1 1,140 (-) — — — 1,157 B. Females 0 5 322 (16) 283 361 II 19 383 (17) 257 530 III 24 476 (15) 350 678 III 78 593 (9) 443 785 IV 126 695 (8) 487 910 V 141 778 (7) 467 980 Y 11 135 824 (7) 654 1,020 VIII 77 896 (9) 676 1,040 VIII 59 937* (9) 802 1,065 IX 56 976 (8) 765 1,085 X 27 989* (13) 890 1,085 X X 16 1,023 (31) 642 1,170 XIII 3 1,096 (7) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVII 2 1,081 (47) 1,035 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVII 0 — — — — — — — — — — — — — — — — — —		XII	13	1,079 (9)	1,030	1,125	1,044	
XV 9 1,088 (15) 1,008 1,127 1,101 XVI 6 1,091 (20) 1,035 1,165 1,115 XVIII 3 1,089 (2) 1,086 1,089 1,126 XVIII 1 1,130 (-) 1,136 XIX 0 1,144 XX 2 1,060 (21) 1,039 1,080 1,151 XXI 1 1,140 (-) 1,157 B. Females 0 5 322 (16) 283 361 I 19 383 (17) 257 530 II 24 476 (15) 350 678 III 78 593 (9) 443 785 IV 126 695 (8) 487 910 V 141 778 (7) 467 980 VI 135 824 (7) 654 1,020 VII 77 896 (9) 676 1,040 VIII 59 937* (9) 802 1,065 IX 56 976 (8) 765 1,085 X 27 989* (13) 890 1,085 X 27 989* (13) 890 1,085 XI 16 1,023 (31) 642 1,170 XIII 3 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVII 2 1,081 (47) 1,035 1,112 XVII 0 XXX 0 XXI 0 XXI 0 C. Males 0 0 0 II 0 III 0		XIII	18	1,079 (6)	1,029	1,123	1,066	
XVII 6 1,091 (20) 1,035 1,165 1,115 XVIII 3 1,089 (2) 1,086 1,089 1,126 XVIII 1 1,130 (-) 1,136 XIX 0 1,144 XX 2 1,060 (21) 1,039 1,080 1,151 XXII 1 1,140 (-) 1,157 B. Females 0 5 322 (16) 283 361 I 19 383 (17) 257 530 III 24 476 (15) 350 678 III 78 593 (9) 443 785 IV 126 695 (8) 487 910 V 141 778 (7) 467 980 VI 135 824 (7) 467 980 VI 135 824 (7) 654 1,020 VIII 77 896 (9) 676 1,040 VIII 59 937* (9) 802 1,065 IX 56 976 (8) 765 1,085 X 27 989* (13) 890 1,085 X 27 989* (13) 890 1,085 XI 16 1,023 (31) 642 1,170 XIII 3 1,096 (7) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVI 2 1,081 (47) 1,035 1,128 XVII 0 XXX 0 XXI 0 II 0 0 V 1 1 992 (-)		XIV	13	1,092 (15)	1,010	1,222	1,085	
XVII		XV	9	1,088 (15)	1,008	1,127	1,101	
XVIII 1 1,130 (-)		XVI	6	1,091 (20)	1,035	1,165	1,115	
XIX		XVII	3	1,089 (2)	1,086	1,089	1,126	
XX		XVIII	1	1,130 (-)	_	_	1,136	
Name		XIX	0	_	_	_	1,144	
Name		XX	2	1,060 (21)	1,039	1,080	1,151	
0 5 322 (16) 283 361 I 19 383 (17) 257 530 III 24 476 (15) 350 678 IIII 78 593 (9) 443 785 IV 126 695 (8) 487 910 V 141 778 (7) 467 980 VI 135 824 (7) 654 1,020 VIII 77 896 (9) 676 1,040 VIII 59 937* (9) 802 1,065 IX 56 976 (8) 765 1,085 X 27 989* (13) 890 1,085 X 1 16 1,023 (31) 642 1,170 XIII 3 1,096 (7) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVI 2 1,081 (47) 1,035 1,128 XVIII 0 — — — — XXX 0 — — — — — — — XXX 0 — — — — — — — — XXX 0 — — — — — — — — — XXX 0 — — — — — — — — — — — II 0 — — — — — — — — — — — III 0 — — — — — — — — — — — — — — — — —		XXI	1			_	1,157	
0 5 322 (16) 283 361 I 19 383 (17) 257 530 III 24 476 (15) 350 678 IIII 78 593 (9) 443 785 IV 126 695 (8) 487 910 V 141 778 (7) 467 980 VI 135 824 (7) 654 1,020 VIII 77 896 (9) 676 1,040 VIII 59 937* (9) 802 1,065 IX 56 976 (8) 765 1,085 X 27 989* (13) 890 1,085 X 1 16 1,023 (31) 642 1,170 XIII 3 1,096 (7) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVI 2 1,081 (47) 1,035 1,128 XVIII 0 — — — — XXX 0 — — — — — — — XXX 0 — — — — — — — — XXX 0 — — — — — — — — — XXX 0 — — — — — — — — — — — II 0 — — — — — — — — — — — III 0 — — — — — — — — — — — — — — — — —	В	Females						
I	-		5	322 (16)	283	361		
II		ī		383 (17)				
III								
IV 126 695 (8) 487 910 V 141 778 (7) 467 980 VI 135 824 (7) 654 1,020 VII 77 896 (9) 676 1,040 VIII 59 937*(9) 802 1,065 IX 56 976 (8) 765 1,085 X 27 989*(13) 890 1,085 XI 16 1,023 (31) 642 1,170 XII 3 1,096 (7) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVI 2 1,081 (47) 1,035 1,128 XVIII 0 XXX 0 XXI 0 II 0 0 II 0 0 II 0 0 II 0 0								
V 141 778 (7) 467 980 VI 135 824 (7) 654 1,020 VII 77 896 (9) 676 1,040 VIII 59 937* (9) 802 1,065 IX 56 976 (8) 765 1,085 X 27 989* (13) 890 1,085 XI 16 1,023 (31) 642 1,170 XII 3 1,096 (7) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVI 2 1,081 (47) 1,035 1,128 XVIII 0 — — — — XVIII 0 — — — — XXX 0 — — — — XXX 0 — — — — XXX 0 — — — — C. Males O O O — — — — — II 0 — — — — II 0 — — — — III 0 — — — — III 0 — — — — III 0 — — — — IV 0 — — — — — V 1 992 (—) — — —								
VI 135 824 (7) 654 1,020 VII 77 896 (9) 676 1,040 VIII 59 937*(9) 802 1,065 IX 56 976 (8) 765 1,085 X 27 989*(13) 890 1,085 XI 16 1,023 (31) 642 1,170 XII 3 1,096 (7) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVI 2 1,086 (38) 1,048 1,124 XVI 2 1,081 (47) 1,035 1,128 XVIII 0 XIX 0 XXX 0 XXX 0 XXX 0 I 0 0 II 0 0 II 0 0 II 0 II 0 0								
VII 77 896 (9) 676 1,040 VIII 59 937* (9) 802 1,065 IX 56 976 (8) 765 1,085 X 27 989* (13) 890 1,085 XI 16 1,023 (31) 642 1,170 XII 3 1,096 (7) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVII 2 1,081 (47) 1,035 1,128 XVIII 0 - - - XIX 0 - - - XXIX 0 - - - XXI								
VIII 59 937*(9) 802 1,065 IX 56 976 (8) 765 1,085 X 27 989*(13) 890 1,085 XI 16 1,023 (31) 642 1,170 XII 3 1,096 (7) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVI 2 1,081 (47) 1,035 1,128 XVIII 0 XVIII 0 XIX 0 XXX 0 XXX 0 XXI 0 II 0 992 (-)								
IX 56 976 (8) 765 1,085 X 27 989*(13) 890 1,085 XI 16 1,023 (31) 642 1,170 XII 3 1,096 (7) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVI 2 1,081 (47) 1,035 1,128 XVIII 0 XVIII 0 XIX 0 XXX 0 XXX 0 XXI 0 I 0 0 I 0 0 II 0 0								
X 27 989*(13) 890 1,085 XI 16 1,023 (31) 642 1,170 XII 3 1,096 (7) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVI 2 1,081 (47) 1,035 1,128 XVIII 0 XIX 0 XIX 0 XXX 0								
XI 16 1,023 (31) 642 1,170 XII 3 1,096 (7) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVI 2 1,081 (47) 1,035 1,128 XVII 0 XVIII 0 XIX 0 XXX 0 XXX 0 XXI 0 II 0 0 III 0 0								
XII 3 1,096 (7) 1,085 1,110 XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVI 2 1,081 (47) 1,035 1,128 XVII 0 XVIII 0 XIX 0 XXX 0 XXX 0 XXI 0 C. Males 0 0 0 I 0 0 II 0 0								
XIII 5 1,054 (12) 1,029 1,100 XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVI 2 1,081 (47) 1,035 1,128 XVIII 0 XVIII 0 XIX 0 XXX 0 XXI 0 XXI 0 I 0 0 II 0 II 0 II 0 II 0 II 0 II 0 992 (-)								
XIV 3 1,110 (20) 1,082 1,150 XV 2 1,086 (38) 1,048 1,124 XVII 2 1,081 (47) 1,035 1,128 XVIII 0 XVIII 0 XIX 0 XXX 0 XXI 0 XXI 0 I 0 0 II 0 II 0 II 0 II 0 II 0 992 (-)								
XV 2 1,086 (38) 1,048 1,124 XVI 2 1,081 (47) 1,035 1,128 XVIII 0 XVIIII 0 XIX 0 XXX 0 XXI 0 XXI 0 II 0 II 0 II 0 II 0 II 0 II 0 992 (-)								
XVI 2 1,081 (47) 1,035 1,128 XVIII 0 XVIIII 0 XIX 0 XXX 0 XXI 0 XXI 0 I 0 0 II 0 992 (-)			2					
XVII 0			2					
XVIII 0 XIX 0 XXX 0 XXX 0				_	_	_		
XIX 0 XXX 0				_	_	_		
XX				_		_		
XXI 0				_	_	_		
0 0			0	_	_	_		
0 0	C	Males						
I 0			0	_ ,	_	_		
II 0				_	_	_		
III 0 V 1 992 (-)				_	_	_		
IV 0 V 1 992 (-)				_ *	_			
V 1 992 (-)				_	_	_		
				992 (_)	_			
2 7,000 (20)					1.060	1.110		
	_				-,000	*,***		_

HOOD AND SCHLIEDER: GAG LIFE HISTORY

345

Table 3. Continued

Age	N	Observed Mean TL (SE)	Min TL	Max TL	Predicted TL
VII	1	946 (-)		_	
VIII	4	1,019 (22)	971	1,067	
IX	13	1,002 (17)	865	1,085	
X	21	1,070 (7)	1,018	1,129	
XI	14	1,068 (13)	998	1,150	
XII	9	1,075 (12)	1,030	1,125	
XIII	12	1,089 (6)	1,050	1,123	
XIV	10	1,088 (18)	1,010	1,222	
XV	7	1,088 (17)	1,008	1,127	
XVI	4	1,096 (24)	1,059	1,165	
XVII	3	1,089 (2)	1,086	1,094	and the second
XVIII	Marie and the state of	1,130 (-)	Contractive Contraction	AND PARTY AND DESCRIPTION OF THE PERSON	STATE AND STREET
XIX	0	_		_	
XX	2	1,059 (21)	1,039	1,080	
XXI		1,140 (-)			