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Age, Growth, Mortality, and Reproduction of Roughtongue Bass, *Pronotogrammus martinicensis* (Serranidae), in the Northeastern Gulf of Mexico

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The inaccessibility of outer continental shelf reefs has made it difficult to investigate the biology of *Pronotogrammus martinicensis*, a small sea bass known to be numerous and widely distributed in such habitat. This study takes advantage of a series of cruises in the northeastern Gulf of Mexico that collected 1,485 individuals. Fish were collected over or in the vicinity of reef habitats with hook and line, otter trawl, and rotenone. We present a preliminary validation of an otolith ageing method and report that *P. martinicensis* reached a maximum size of 143 mm standard length (SL), grew to about 50% of this size within their first year, and lived to a maximum age of 15 yr. Size at age data ($n = 490$) fitted to the von Bertalanffy growth model yielded the predictive equation: $SL_t = 106.3(1 - e^{[-0.641\{t-0.646\}]})$, where t = age in years. Gonad histology ($n = 333$) was examined to confirm that *P. martinicensis* is a protogynous, monandric hermaphrodite. We found no evidence of simultaneous hermaphroditism, which had been tentatively proposed in a previous study. Most *P. martinicensis* matured as females in their second year (age 1), primary oocytes developed asynchronously into secondary oocytes, and females were batch spawners. Males were postmaturational. Seminiferous tissue formed as early as age 1, but, although the rate of sex change is unknown, most fish did not function as a male until age 3 or age 4. These data provide age-based benchmarks of a common reef fish species living on the outer continental shelf of the tropical western North Atlantic Ocean.

Roughtongue bass, *Pronotogrammus (Holanthias) martinicensis* (Guichenot), is a widely distributed and numerically dominant species inhabiting outer continental shelf reefs (50 to 230 m) of the Gulf of Mexico, western North Atlantic Ocean, and Caribbean Sea [Bullock and Smith, 1991 (and references therein); Koenig et al., 2000]. It is an important trophic link between secondary production and secondary consumers, feeding on small zooplankton and preyed upon by fishery species such as red snapper (*Lutjanus campechanus*) and larger grouper species (Serranidae) (Bullock and Smith, 1991). *Pronotogrammus martinicensis* is also part of a small marine ornamental fishery because it is brightly colored and valuable to aquarium hobbyists (C. Cole, Chris's Marine, LLC, pers. comm.; F. Young, Dynasty Marine Associates, pers. comm.).

Coleman (1981) reported that *P. martinicensis* is a protogynous hermaphrodite, on the basis of evidence that females were smaller than males and transitional individuals were intermediate in size. Although such size structure data can be confounded by variable growth rates (Sadovy and Shapiro, 1987), Coleman (1981) also reported that that all testes examined (n = 54) showed evidence of an ''ovarian'' lumen, leaving little doubt that this species is monandric (i.e., all males are secondary). Left unclear, however, was whether *P. martinicensis* is capable of simultaneous egg and spermatozoa production, because Coleman (1981:893) refers to a specimen in which ''both spermatogenesis and oogenesis appear to be occurring simultaneously.'' There are, however, several steps in the process of gametogenesis, and Coleman's singular observation did not directly state that this individual appeared capable of functioning as a male and female at the same time.

This study characterizes the life history of *P. martinicensis* from material collected in the drowned reef zone of the northeastern Gulf of Mexico. Size and sex data are compared with data from Coleman (1981), and the age data, which are new for this species, are used to describe growth, longevity, and mortality.

Samples were collected during a series of cruises by the U.S. Geological Survey (USGS) from 1997 to 2002. These cruises were designed to develop a holistic understanding of shelf-edge deep-reef communities that exist in areas of ongoing or potential hydrocarbon exploration and development (Weaver et al., 2002). In this context, abundant and ubiquitous components of the fauna, such as *P. martinicensis,* may serve as important indicators of the health, stability, and resilience to disturbance of shelf-edge reef communities. Therefore, the data in this study establish a biological reference point for management of this ecosystem as well.

Materials and Methods

USGS cruises sampled fish over and near reefs about 50–200 m deep and within an area of the northeastern Gulf of Mexico bounded by latitudes 29°11.3′ and 29°42.0′N and longitudes 85°40.7′and 88°20.3′W. Most fish were collected by small unbaited rigs [i.e., Sabiki©, Piscatore© rigs, referred to herein as H & L (= hook and line)] while anchored in association with reef habitat at 12 different locations within this area. These rigs were dropped to the bottom with weights (6–16 ounces [170–455 g] depending on water current and depth) and fished vertically just off the substrate to imitate zooplankton. A variety of hook sizes (3, 4, 6, 8, 10) were used and all hook sizes collected *P. martinicensis*. Additional fish were collected with a small-mesh (3.8-cm mesh body and a 0.6-cm mesh liner), 4.9-m semiballoon otter trawl, which was towed over soft substrates adjacent to these reefs. Finally, collections were augmented using a remote-operated vehicle (ROV) equipped with a pump and suction tube (38.1-mm inner diameter) filled with rotenone; the contents of the tube were released near the bottom and dead fish were immediately vacuumed up and brought to the surface.

The disposition of these samples varied (Table 1). Most fish were either frozen or fixed in 10% phosphate-buffered formalin while at sea. Frozen fish were measured to the nearest millimeter standard length (SL), weighed to the nearest 0.01 g total body weight (BW), and the sagittal otoliths were removed, cleaned, and stored dry in vials. Fixed fish were measured to the nearest millimeter SL, weighed to the nearest 0.01 g BW and gonad weight (GW), and the gonad was removed, rinsed, and stored in 70% ethyl alcohol (EtOH). Fish from two cruises were processed directly, while at sea: measured to the nearest millimeter SL, weighed to the nearest 1 g BW, and both the gonads and otoliths were removed and processed (as above). A weight–length relationship was fitted to the nonlinear model, $\mathrm{BW} = a \times \mathrm{SL}^b$, by least-squares regression.

We report ages, in years, as estimated from sectioned sagittal otoliths. Sections were cut from the left otolith core, approximately 350–400 µm thick, along the transverse plane, with a low-speed saw equipped with a diamond wafering blade. These were mounted on glass slides. The number of complete annuli were counted by a single reader (AKR), and the the presence or absence of an annulus on the margin was also recorded.

Table 1. The disposition of 1,485 roughtongue bass, *Pronotogrammus martinicensis*, collected in the northeastern Gulf of Mexico. Year and month refer to cruise dates. The number of fish are tabulated as to whether only standard length (SL only, n = 704), only SL and age (SL + age, n = 448), only SL and sex (SL + sex, n = 291), or SL, age, and sex (All data, n = 42) were determined. ND = no cruise dates recorded for these fish.

Year	Month	SL only	SL + age	SL + sex	All data
1997	8	6		48	
1998	8			17	
	10	25	39		
1999	2	88	145		
	5	45	62	2	
	6	88	131	29	
2000	3	78	13	71	
	9	59	21		
2001	5	231	34	29	25
2002	8	4	3	42	17
ND	ND	80		53	

Periodicity of annulus formation was examined using two related analyses. In both cases, only otoliths with three or four completely formed annuli were used, so as to minimize age-specific results. First, those individuals with an incomplete, opaque annulus on the otolith edge were plotted, as a percentage of all individuals examined, by sampling month. Second, the marginal increment (MI) distance was plotted as an average value ± 95% confidence limits (c.l.) by sampling month. For MI analysis, MI = sectioned otolith radius–sectioned marginal distance (SOR-SMD)/SOR, where SOR = the distance from the otolith core to the outer edge along the transverse groove, and SMD = the distance from the core to the middle of the last complete annulus along the same axis. These measurements were determined to the nearest micrometer using a dissecting microscope equipped with a video system and image analysis software. These edge or MI values were not available for all months, so demonstrating an unambiguous annual pattern was not possible. Instead, the data were examined visually for a pattern consistent with a monocyclic, annual pattern, and an analysis of variance (ANOVA) was used to test if the monthly MI means were at least significantly different from one another.

Final ages, in years, were assigned as the number of complete annuli plus 0.5 yr. The addition of this constant increases the age estimate to account for a median amount of growth beyond the last complete annulus. Growth was modeled using the von Bertalanffy growth equation: $L_t = L_\infty\left(1 - e^{[-K\{t-t_0\}]}\right)$, where L_t is the predicted SL at age t, L_∞ is the asymptotic SL, K is the Brody growth coefficient, t is the age in years, and t_0 is the predicted age at which the average SL is zero. Annual survival estimates ($\hat{S}$) were derived using the estimator from Robson and Chapman (1961): $\hat{S} = \sum_x^k xf_x/(\sum_x^k f_x + \sum_x^k xf_x - 1)$, where x is the youngest age (in years) fully vulnerable to fishing (also referred to as t_r in Table 2), f_x is the number of fish per age-class x, and k is the oldest age class. Separate estimates of $\hat{S}$ were calculated for all aged fish and for aged fish from H & L collections only, the latter to standardize the dominant collecting gear. Survival estimates were converted to instantaneous mortality rates by the relationship: $\hat{M} = -\ln(\hat{S})$. Since there is no significant fishery for such small seabasses, total mortality was considered attributable only to natural sources.

Sexual development was examined using histological methods. Fixed gonads, initially stored in 70% EtOH, were dehydrated in a series of increasing concentrations of EtOH, embedded in paraffin, sectioned along the transverse plane (4 µm thick), and stained with hematoxylin and eosin. Two readers (RSM, PET) independently classified individuals as female, male, or transitional on the basis of the presence of ovarian tissue, seminiferous tissue, or both, respectively.

Size, age, and maturity data were fitted to the logistic equation: $Y = 1/[1 + \exp(-\alpha - \beta \times X])$, where $Y = 0$ for females or 1 for transitionals and males, α = the intercept, and β = the slope of the curve, and X = size or age. The size or age at 50% transformation was calculated as α/β. Model parameters were estimated by the logistic procedure of SAS software (Allison, 1999).

The most advanced stage of oogenesis was noted for all females—particularly the demonstration of final oocyte maturation (i.e., migration or breakdown of the nucleus), as this would indicate imminent spawning. Postovulatory follicles, which would indicate that spawning occurred within hours or days, were also noted. The most advanced stages of oogenesis and spermatogenesis were noted for all transitionals to check for simultaneous hermaphroditism; criteria for simultaneous hermaphroditism would be the presence of advanced germ cells (i.e., vitellogenesis and spermatozoa) to indicate the capacity for a single individual to produce eggs and spermatozoa contemporaneously.

TABLE 2. Age frequency of roughtongue bass, *Pronotogrammus martinicensis*, collected by all sampling gears and by hook and line (H & L) rigs only. $\hat{M}$ = the estimated natural mortality rate using the Robson and Chapman (1961) estimator (see text for details). Age at full recruitment (t_r) was set at 1 or 3 yr.

	Number of fish	
Age (yr)	All gears	H & L
0	8	2
1	44	27
2	54	33
3	171	108
4	82	40
5	60	38
6	23	18
7	18	9
8	13	12
9	7	5
10	5	3
11	2	1
12	1	1
13	1	1
14	0	0
15	1	1
$\hat{M}$		
$t_r = 1$	0.304	0.295
$t_r = 3$	0.542	0.509

Batch fecundity, the number of eggs produced per spawning event, was calculated from counts of hydrated oocytes following the methods of McBride et al. (2002). Briefly, batch fecundity was computed as a product of relative fecundity and total GW. Relative fecundity was estimated as the total number of hydrated oocytes in the right ovary lobe divided by the weight of the right ovary lobe. The total number of the hydrated oocytes was counted six times per individual and the range among all counts was less than 2%.

RESULTS

A total of 1,485 *P. martinicensis* was collected at 12 different locations on the outer continental shelf, 62–185 m, in the northeast Gulf of Mexico, offshore of Alabama and the west coast of Florida (Table 1). They were collected during all sampling months: February, March, May, June, Aug., Sep., and Oct. Fish ranged in size from 17 to 143 mm SL (Fig. 1).

Most fish were collected by H & L rigs (914 of 1,010 fish with the type of sampling gear recorded). These fish were generally larger, ranging from 35 to 143 mm SL (Fig. 1), than fish collected by other gears. The fish sizes caught by trawl were 17–88 mm SL (n = 27) and the sizes caught by ROV were 29–96 mm SL

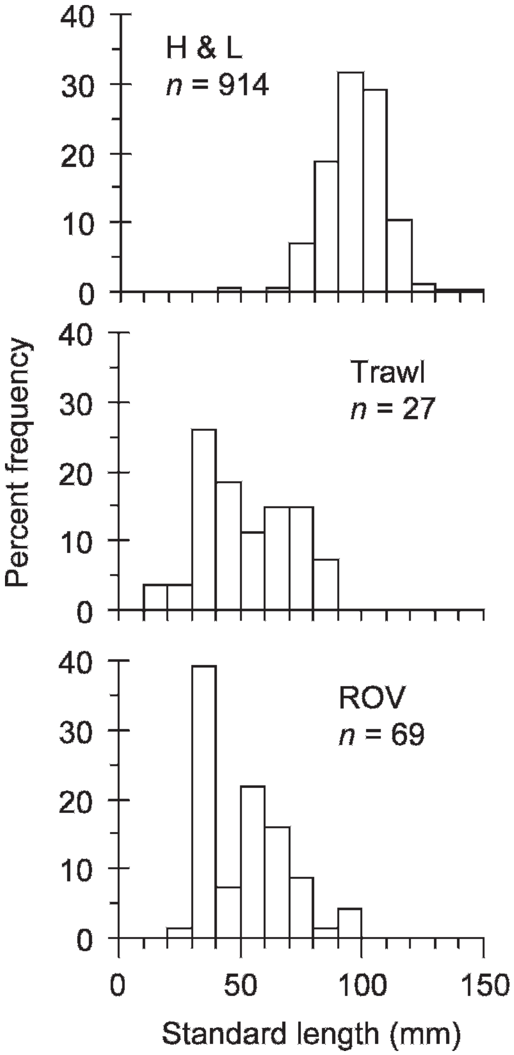

Fig. 1. Percentage length frequencies of roughtongue bass, *Pronotogrammus martinicensis*, collected by three different gears: hook and line (H & L) rigs, trawl, or remote-operated vehicle (ROV); n = number of fish.

(n = 69). The longest fish captured (143 mm SL) weighed 90.0 g. Fish from 29 to 143 mm SL (n = 1,366) were weighed and used to develop the predictive weight–length equation: BW = $0.000090^{*}(\mathrm{SL})^{2.785}$ ($r^2 = 0.92$, $P < 0.01$).

Regularly spaced annuli were evident in the sectioned otoliths (Fig. 2A, B). During spring, most age-3 and age-4 fish had an opaque zone (= annulus) on the margin and the MI was largest (Fig. 3). During autumn, most age-3 and age-4 fish did not have an opaque zone on their margin and the MI was smaller. The MI differed significantly between months (ANOVA; F_s = 2.80; P = 0.012). Although preliminary in nature, these monthly patterns were consistent with a single, annual cycle with a new annulus formed in summer.

Fish from 31 to 143 mm SL were aged, ranging from 0 (i.e., young-of-the-year) to 15 yr old (Fig. 4). These data fit the von Bertalanffy growth model reasonably well ($r^2 = 0.49$, n = 490, $P < 0.01$), resulting in the predictive equation: $L_t = 106.3(1 - e^{[-0.641\{t-0.646\}]})$.

The modal age was 3, both for all fish aged (n = 490) and for those aged from H & L collections only (n = 299). Selection of the age at full recruitment (t_r) had more effect on the estimate of survival than the effect of pooling gears (Table 2). When $t_r = 1$, which excludes only young-of-the-year fish, the survivorship estimate was 73.8% ± 2.1% (mean ± 95% c.l.) per year using all aged fish; it was 74.5% ± 2.6% per year using fish collected with H & L only. When $t_r = 3$, which excludes all ages lower than the peak age frequency, the survivorship estimate was much lower: 58.1% ± 3.3% (mean ± 95% c.l.) per year using all aged fish and 60.1% ± 4.0% per year using fish collected with H & L only. These survival rate estimates corresponded to natural mortality rates of approximately 0.3 yr^{-1} ($t_r = 1$) or 0.5 yr^{-1} ($t_r = 3$) (Table 2).

Five females with hydrated oocytes were observed in March and May, indicating spring spawning (Fig. 2C). Females may not spawn, or may spawn less frequently, during summer, on the basis of our observation that the females collected in June and Aug. had no hydrated oocytes. Females were not collected in any other month, so spawning seasonality remains relatively undefined.

During spring, a mix of oocyte stages was evident, indicating asynchronous oocyte development and indeterminate fecundity (Fig. 2C). Four fish collected in the spring months were observed with postovulatory follicles. These females also had hydrated oocytes, which indicated a batch spawning frequency of daily or every few days for at least some individuals. Batch fecundity was calculated for three females collected in May 2001: 149 oocytes per batch for a 62 mm SL (no age) fish; 199 oocytes per batch for a 55 mm SL (age 1) fish; 393 oocytes per batch for a 58 mm SL (no age) fish.

Female *P. martinicensis* were smaller and younger than males, and transitional fish were intermediate and overlapping in size and age of both sexes (Table 3; Fig. 5). The size and age at 50% transformation were calculated as 76.3 mm SL and 1.0 yr, respectively.

Transitional specimens were collected during March, May, June, and Aug. Among these fish, there was no obvious progression of seminiferous

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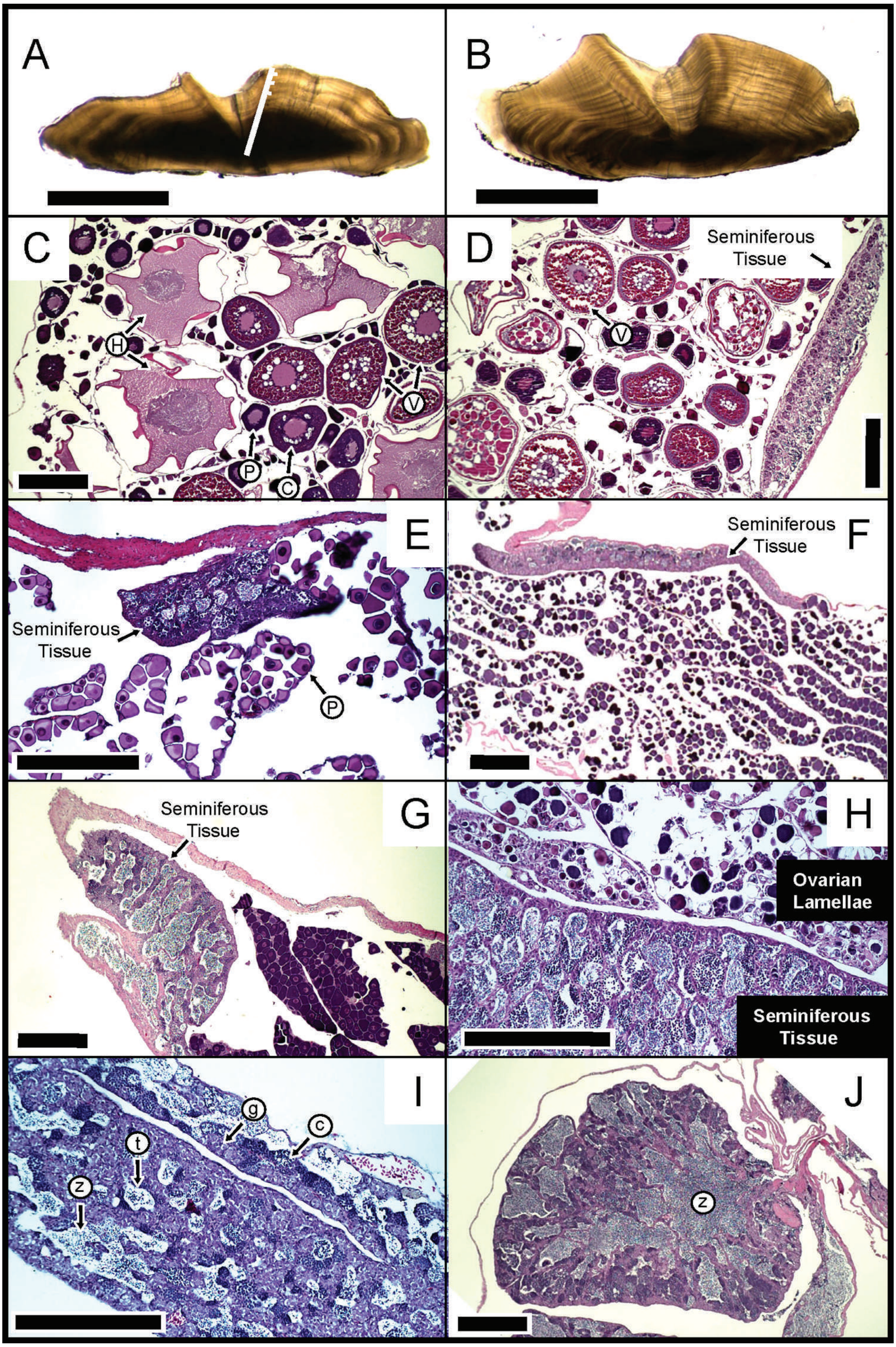

Fig. 2. Sectioned otoliths (A, B) and gonad histology (C–J) of roughtongue bass, *Pronotogrammus martinicensis.* (A) A 98-mm, age-3 fish (sex unknown) collected February 1999; the diagonal white line indicates the radius of measurement for marginal increment analysis and appendent dashes indicate the locations of three complete annuli. (B) The oldest fish encountered in this study: a 104-mm, age-15 fish (sex unknown, presumably male but no histology available) collected May 2001. (C) A 73-mm (no age) actively spawning female (i.e., with hydrated

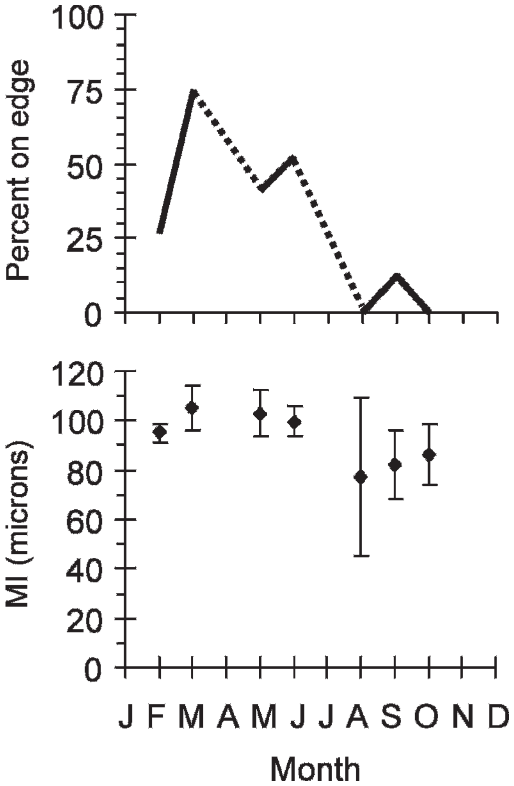

Fig. 3. Edge analysis (top panel, monthly % fish with opaque zone on otolith edge) and marginal increment (MI) analysis (bottom panel, monthly average MI ± 95% confidence limits) using sectioned sagittal otoliths of roughtongue bass, *Pronotogrammus martinicensis.* All fish were either age 3 or age 4 to standardize the method.

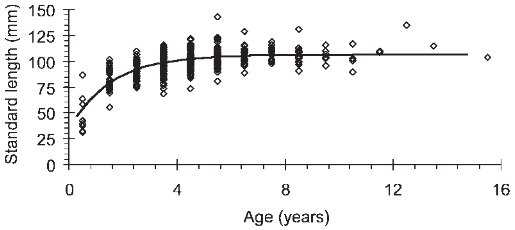

Fig. 4. Length at age for 490 roughtongue bass, *Pronotogrammus martinicensis.* The solid line is the predicted length at age curve from the von Bertalanffy growth model (see Results for fitted equation).

tissue development from March to Aug. Atretic oocytes were common but massive atresia was not a defining characteristic of these transitionals; instead, previtellogenic oocytes were typically present together with seminiferous tissue of varying stages of spermatogenesis. A developmental sequence was noted among transitional fish examined: seminiferous tissue appeared to originate at a discrete point along the periphery of the gonad and expanded inward without mixing with ovarian tissue (Fig. 2E–H). Some, but not all, transitionals had expansive and discontinuous lobules filled with spermatozoa (i.e., spermiation). In a single transitional individual, a batch of oocytes was present with coalescing yolk (Fig. 2D), which indicated that this batch was entering final oocyte maturation. Nonetheless, in this individual, only spermatogonia and spermatocytes were evident in its seminiferous tissue, so the criterion for simultaneous hermaphroditism was not met. An ovarian lumen was evident in immature and mature males (Fig. 2I, J), so there was no evidence of primary males.

Discussion

Pronotogrammus martinicensis was readily sampled using small, unbaited hooks. Smaller and younger fish, mostly females and transitionals, were underrepresented by H & L, but they were collected by additional sampling with trawls and an ROV sampling method.

←

oocytes) collected May 2001. (D) A 74-mm (no age) transitional fish collected March 2000; this fish was still spawning as a female, as evident from a batch of oocytes with coalescing yolk, whereas the seminiferous tissue (arrow) contained only crypts of spermatogonia and spermatocytes. (E) A 98-mm, age-3 transitional fish collected May 2001; this image shows all of the seminiferous tissue present, evidently just forming in this fish. (F) A 94-mm, age-3 transitional fish collected May 2001; the seminiferous tissue is more extensive here (vs. Fig. 2E) but it is still not mixed with ovarian lamellae. (G) A 73-mm, age-1 transitional fish collected Aug. 2002; no atresia was evident in the ovarian tissue (right half of image) even though the seminiferous tissue was well developed. (H) A 93-mm, no age transitional fish collected March 2000; atresia within ovarian tissue is extensive (upper part of image), the seminiferous tissue was extensive, and spermatogenesis was advanced. (I) An 81-mm, age-2 male collected May 2001; spermiation in this individual was limited and this male may be immature. (J) A 96-mm, no age male collected May 2001; spermiation within an extensive, discontinuous lobule is evident in the center of the tissue. The major stages of oocyte development are indicated by capitalized letters: perinucleolar (P), cortical alveolar (C) (= yolk vesicle), vitellogenic (V) (= yolked), hydration (H). Symbols for spermatogenesis are: spermatogonia (g), spermatocytes (c), spermatids (t), and tailed sperm (z). Scale bars for otoliths (A, B) are 1-mm long; scale bars for gonads (C–J) are 0.25-mm long. Fish sizes are millimeter standard length. Age is in years.

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Table 3. Sex-specific size (A) and age (B) of roughtongue bass, *Pronotogrammus martinicensis*, collected in the northeastern Gulf of Mexico. Tabulated data include mean (Mean), 95% confidence limits (95% c.l.), median (Med.), minimum (Min.), maximum (Max.), and number of fish (n). Sample sizes do not reflect sex ratios observed in the field because most fish were collected by H & L gear, which selected larger fish, predominantly males (see Fig. 1).

	Mean + 95% c.l.	Med. (Min.–Max.)	n
(A) Standard length (mm)			
Female	65.9 ± 4.8	68 (31–106)	53
Transitional	85.3 ± 2.8	85 (71–104)	33
Male	100.3 ± 1.4	99 (73–143)	247
(B) Age (yr)			
Female	0.67 ± 0.5	1 (0–1)	6
Transitional	2.0 ± 1.2	2 (1–3)	5
Male	4.2 ± 0.8	4 (1–12)	31

In analyzing data collected during the same USGS cruises, Weaver et al. (2002) reported that *P. martinicensis* is abundant and widely distributed in the northeastern Gulf of Mexico. ROV videotapes and gut content analysis showed this species to be a diurnally active mesoplanktivore associated mostly with the base and crest of high profile reefs (Weaver et al., 2002). This species was observed at 38 of 41 site visits in 1997, 1999, and 2000, with as many as 21 fish per minute observed on the videotapes; in total, it was the most numerous species observed on videotapes from these cruises (Weaver et al., 2002). Previously, *P. martinicensis* had also been noted as common or abundant on outer shelf reefs of the northern Gulf of Mexico (Dennis and Bright, 1988a,b; Koenig et al., 2000), the western North Atlantic (Lindquist and Clavijo, 1993), and the Caribbean Sea (Colin, 1974).

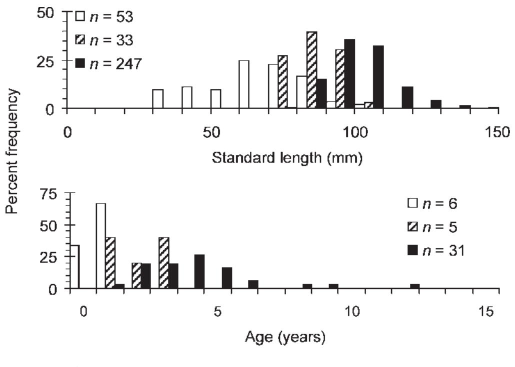

Fig. 5. Size and age frequency of female (open bars), transitional (hatched bars), and male (filled bars) roughtongue bass, *Pronotogrammus martinicensis*; n = number of fish.

Pronotogrammus martinicensis is a small but relatively fast-growing serranid. The von Bertalanffy growth model predicts that the average individual reaches half of its asymptotic length (106 mm) and a third of it maximum observed size (143 mm) before 6 mo of age. Previous reports of maximum size were smaller [Anderson and Heemstra, 1980 (97 mm SL); Coleman, 1981 (132 mm SL)] and sizes estimated from video were much smaller still (Lindquist and Clavijo, 1993).

Although the edge and marginal increment analyses were consistent with one annulus per year, this validation of the otolith ageing method should be considered preliminary, until more months are covered and more age classes can be included, or more direct methods become available to test the frequency of annulus deposition (Campana, 2001).

Comparatively, *P. martinicensis* lives longer (15 yr) than other small serranids [*Diplectrum formosum* (6 yr), *Centropristis striata* (7 yr); Bortone, 1971; Hood et al., 1994; McGovern et al., 2002], but has a shorter life span than other, much larger serranids [*Epinephelus morio* (18 yr), *Mycteroperca microlepis* (21 yr), *Mycteroperca phenax* (30 yr), *Mycteroperca bonaci* (33 yr); Hood and Schlieder, 1992; Johnson and Collins, 1994; Crabtree and Bullock, 1998; Harris et al., 2002]. At the population level, the relative longevity of *P. martinicensis* may contribute to its high abundance and wide distribution. Relatively long life and early maturation means that spawning biomass accumulates and can take advantage of stochastic periods when propagule survival and dispersal are favorable (Secor, 2007). Recruitment of reef fish tends to be sporadic but a longer maximum life span enhances the ability for a population to persist, which, at a community level, leads to high species richness (Sale, 2004). Moreover, when considering that *P. martinicensis* is common in the diet of several larger predators (Bullock and Smith, 1991), especially heavily exploited fishery species such as snappers (Lutjanidae) and groupers (Serranidae), it may be postulated that *P. martinicensis* is living longer today, during a period when the population sizes of its predators are estimated to be low (Stanley and Scarborough-Bull 2003; Patterson et al., 2007). Thus, our estimate of longevity is a valuable benchmark to examine in the future for the potential of top-down, predatory control of age structure of unfished populations of reef fish.

Estimates of mortality rates from our age data were highly dependent on the assumption of age at recruitment (t_r), which is typically set by inspection of age frequency data. From our data, a case could be made that $t_r = 3$, the highest age frequency, which defines the descending limb of ages. However, simple estimators of mortality, such as that reviewed by Hewitt and Hoenig [2005; ln [$\hat{M}$] = 1.44 − 0.982*ln(maximum age)], predict an $\hat{M}$ rate closer to that estimated in this study when $t_r = 1$. Thus, we consider these estimates of $\hat{M}$ to be preliminary. They may be confounded by methodological issues, such that t_r or gear selectivity needs to be directly measured, or there may be biological issues operating here. In particular, the social structure of *P. martinicensis*, particularly its dominant-male mating system, may result in lower mortality among the oldest terminal males and thereby confound a simple estimate of $\hat{M}$ across all age clases older than t_r. There may also be spatial variation in age structure, whereby the oldest fish observed here (15 yr) is not typical among reefs in this region. In this regard, Allman (2007) showed variation of vermillion snapper, *Rhomboplites aurorubens*, age structure in the northeast gulf at the same spatial scale that we sampled here, demonstrating that metapopulation structure can be operating at fairly small scales in the marine environment.

Pronotogrammus martinicensis is a monandric, protogynous hermaphrodite. We saw no evidence of primary males together with terminal males, so we rule out diandric sexual development. Nor did we find any individuals with oocytes in final maturation together with spermiation. Thus, we rule out simultaneous hermaphroditism. Other anthiines are also protogynous hermaphrodites: *Anthias squamipinnis*, *Hemanthias peruanus*, and *Hemanthias vivanus* (Shapiro, 1981; Hastings, 1981; Coleman, 1983), which is a common reproductive mode within the Serranidae.

We also observed that males were all much larger and older than females, suggesting that sex change is postmaturational (i.e., transition to a male occurred only after maturing first as a female). We observed a mean size of transitional *P. martinicensis* that was very similar to that described by Coleman (1981), who noted transitional *P. martinicensis* to range from 73 to 94 mm SL (mean = 81.6 mm). It did not seem that sex change initiates in a single season and proceeded over the course of several months (but less than 1 yr) because we did not see an orderly development of seminiferous tissue consistent with that periodicity. Instead, it appears that sex change is either rapid (days–weeks) and initiates in any of several different months, or it is slow (> 1 yr) and initiates shortly after the spring spawning observed herein. Given the 1–2-yr difference between mean age of females and transitional fish, as well as between transitionals and males, we suspect that the complete transitional period is at least 1 yr.

Regional variations have also been observed in the size at sexual transition in another protogynous anthiines, but, as in the study of Coleman (1981), we did not have sufficient data to examine for intraspecific variation. The size at transition for another small anthiin serranid, *A. squamipinnis*, can vary spatially, ranging from 40 to 65 mm SL, and is under social control, in that the removal of a male will induce a female to change sex (Shapiro, 1981).

Given the wide distribution of *P. martinicensis*, and its importance in the trophic structure of the deep-reef community, further consideration of geographic variation in life history traits should be of interest. Such research is likely to lead to a more process-oriented understanding of the demographic and community structure of fishes on outer continental shelf deep reefs.

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