Age, growth, and reproduction of the littlehead porgy, *Calamus proridens*, from the eastern Gulf of Mexico

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ABSTRACT.—The present study is the first comprehensive examination of the life-history of *Calamus proridens* Jordan and Gilbert, 1884, the littlehead porgy, in the eastern Gulf of Mexico. In total, 1814 *C. proridens,* ranging in fork length from 76 to 361 mm, were collected along the gulf coast of Florida from 2000 through 2007. Length, sex, age, and reproductive state were determined. Length classes included the range of ontogenetic development for both sexes and transitional individuals. Overall sex ratios and sex ratios grouped by length class and age were significantly different from the 1:1 ratio characteristic of gonochoristic species. Females ranged in age from 0 to 6 yrs, while males ranged from 1 to 10 yrs. The von Bertalanffy growth model fitted to all observed data was $L_{(t)} = 306 \times (1 - e^{-0.254 (t + 1.69)})$. Spatially explicit von Bertalanffy growth models (from trawl data only) indicated that fish captured in the central region grew larger than those in the southern region. *Calamus proridens* mature at a young age; 50% of the females collected during the spawning season were mature within their first year (132 mm FL). Histological analysis revealed that *C. proridens* are protogynous hermaphrodites with delimited gonads. Estimates indicated that at age 4 (231 mm FL), approximately 50% of females in the population had transitioned into males. The present study has utility for improving the accuracy of stock assessments of *C. proridens* in the Gulf of Mexico and also has relevance in ecosystem modeling.

The littlehead porgy, *Calamus proridens* Jordan and Gilbert, 1884, is commonly encountered in the commercial and recreational fisheries in the Gulf of Mexico (GOM) and Campeche Bank, Yucatán. *Calamus proridens* has been reported as the most important and abundant member of the family Sparidae in the commercial fishery in the Campeche Bank, Yucatán (Dubovitsky 1977a). *Calamus proridens* occurs in the Atlantic Ocean and GOM from Florida to Louisiana, in the Campeche Bank, Yucatán, and through the Greater Antilles (Randall and Caldwell 1966, Dubovitsky 1977a, Darcy 1986, Pierce and Mahmoudi 2001). They are typically associated with natural or artificial reefs, offshore platforms, and live bottoms consisting of sponges and corals (Darcy 1986, Pierce and Mahmoudi 2001). Their habitat overlaps that of groupers and snappers, and they are often harvested incidentally by the commercial

reef fishery in Florida (Randall and Caldwell 1966, Dubovitsky 1977a, Darcy 1986). *Calamus proridens* are an important intermediate trophic-level component of the nearshore and offshore fish assemblages off the west coast of Florida, serving as a food source for sharks and larger groupers and snappers (Darcy 1986).

Florida has initiated a multi-species ecosystem approach to managing fisheries in an effort to understand how fish assemblages are affected by prolonged harvesting of commercial species (Randall and Caldwell 1966, Darcy 1986, Pierce and Mahmoudi 2001). Despite the incidental harvest of *C. proridens*, no current regulations exist for the species in terms of bag limit, size, or total allowable catch. Recreational harvest of porgies off the west coast of Florida between 2000 and 2013, not including pinfish, *Lagodon rhomboides* (Linnaeus, 1766), red porgy, *Pagrus pagrus* (Linnaeus, 1758), or sheepshead, *Archosargus probatocephalus* (Walbaum, 1792), exceeded 579,000 lb (262,600 kg) (personal communication from the National Marine Fisheries Service, Fisheries Statistics Division, June 2014). Even though *C. proridens* is caught by both commercial and recreational fisheries and is important to the overall reef fish assemblage, life-history information that would help predict the impact of the harvest is limited, especially in the GOM (cf. Dubovitsky 1977a,b, Darcy 1986).

Many sparids are reported to be protandrous (male to female) (Buxton and Garratt 1990, Besseau and Bruslé-Sicard 1995, Lee et al. 2008) or protogynous (female to male) (Huang et al. 1974, Garratt 1986, Buxton and Garratt 1990, Kokokiris et al. 1999) hermaphrodites. Most research on sex-changing fish is focused on species in the families Serranidae (groupers and seabasses) (Coleman 1981, Fischer and Petersen 1987, Shapiro 1987, Cochran and Grier 1991, Bullock et al. 1996, Thurman 2004), Labridae (wrasses) (Warner and Swearer 1991), and Scaridae (parrotfish) (Sadovy de Mitcheson and Liu 2008). Sex change in those families is undelimited—male and female tissues are intermixed or separated within the gonad during the course of sex change. Little research has been conducted on the sex change processes of sparids, which is reported to be delimited, i.e., male and female gonads are separated by connective tissue. Most research conducted on sparids has been on species from South Africa: *Chrysophrys major* (Temminck and Schlegel, 1843), *Chrysoblephus puniceus* (Gilchrist and Thompson, 1908), *Lithognathus mormyrus* (Linnaeus, 1758), and *Acanthopagrus schlegeli* (Bleeker, 1854) (Huang et al. 1974, Garratt 1986, Buxton and Garratt 1990, Besseau and Bruslé-Sicard 1995, Lee et al. 2008) or *P. pagrus* (Pajuelo and Lorenzo 1996, Kokokiris et al. 1999, Hood and Johnson 2000, DeVries 2006, Kokokiris et al. 2006). Little information is available on age and length of *C. proridens* at the time of sex-change, with most information coming from the Campeche Bank (Dubovitsky 1977a,b).

The difficulty of quantifying transition rates and differential growth contributes to the uncertainty of stock assessments in sex-changing fishes and may impact management decisions (Armsworth 2001, Alonzo and Mangel 2004, Davis and Berkson 2005). Additional research on sequential hermaphrodites will increase our understanding of the vulnerability of these species to overfishing (Alonzo and Mangel 2004, DeVries 2006). Hermaphroditic fishes are especially vulnerable to overexploitation, as fisheries typically target larger fish first, leading to the size-specific removal of the terminal sex and disrupting the population's reproductive potential (Crabtree and Bullock 1998, Armsworth 2001, Alonzo and Mangel 2004, Davis and Berkson 2005). Incorporating protogynous life-history information in stock assessments will improve model realism and increase our understanding of how sex-changing species
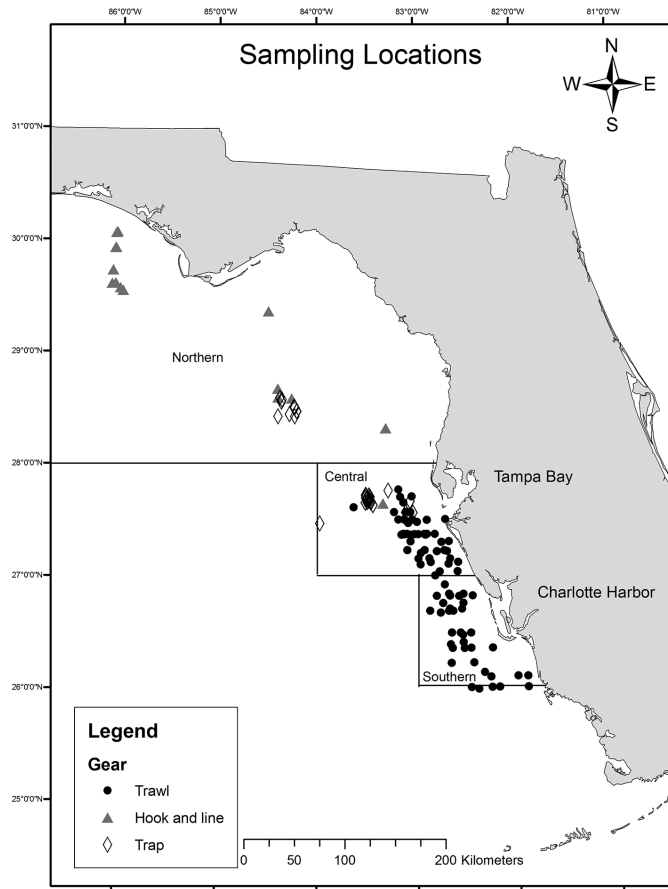
Figure 1. Sampling locations of *Calamus proridens* from the Fish and Wildlife Research Institutes Fisheries-Independent Monitoring (FIM) program's baitfish cruise surveys (●), FIM chevron trap cruises (◊), and hook-and-line samples (▲) from the National Marine Fisheries (NMFS) in Panama City and the Fisheries-Dependant Monitoring program. All fish were collected from 2000–2007.

respond to fishing pressure. The objectives of the present study were to describe the age and growth parameters and reproduction of *C. proridens* from the eastern GOM, focusing on age and length at sexual transition.

Methods

Geographic Coverage and Sample Collections.—Fish were collected from the eastern GOM from 2000 through 2007 (Fig. 1). The majority of fish (*n* = 1640) were collected between 2003 and 2007 during the Fish and Wildlife Research Institute's (FWRI) Fisheries-Independent Monitoring (FIM) program's spring (April and May) and fall (October and November) baitfish surveys using a 65-ft (20-m) balloon trawl (Nelson 2002). The FIM baitfish trawl surveys were designed to characterize nearshore baitfish communities proximal to two nearby estuaries: Tampa

Bay and Charlotte Harbor. Survey effort was stratified into two regions: a central region around Tampa Bay (27°N, 82°30′W) and (27°26′N, 84°W), and a southern region around Charlotte Harbor (26°N, 82°W) and (27°N, 83°W) (Fig. 1). Frequency of samples and depth (6–28 m) were the same between the two regions. To obtain a more comprehensive collection of fish from various months and sizes, fish were also collected using hook-and-line by the National Marine Fisheries Service (NMFS) (n = 40, 2000–2002) and by FWRI's Fisheries-Dependent Monitoring program (n = 54, 2002–2005, 2007). Baited chevron fish traps were also used (n = 80) in 2006 and 2007 (FIM). The chevron traps were 1.7 m long, 1.5 m wide, and 0.6 m deep with 3.8-cm vinyl-clad steel mesh (Collins 1990). All trawls and chevron traps were deployed at randomly selected sites within a predefined area.

During each sampling event, standard (SL), fork (FL), and total (TL) lengths (mm), and total weight (g) of all *C. proridens* were recorded when possible. In addition, the sex of each fish was determined macroscopically in the field. Linear regression was used to determine length-to-length relationships and R^2 values of 0.99 were obtained for all length combinations. Those equations (FL = 1.13 × SL + 1.12, n = 1545; FL = 0.87 × TL − 4.25, n = 1558) were then used to calculate FL when FL was not recorded. The only length reported in the present study is FL because that was the most common length recorded in the field, unless otherwise noted. Length and weight were log transformed and an analysis of covariance (ANCOVA) was used to test for differences between sexes (Ricker 1975, Sokal and Rohlf 1981, Froese 2006).

Age and Growth.—Fish were aged using sectioned and whole sagittal otoliths (Fig. 2). Readability of large whole otoliths can be compromised due to clouding or crowding of rings. To reduce error in readings, 202 otoliths covering a variety of ages were aged whole and then sectioned and aged again to identify the limits of aging using whole otoliths. Ages from whole otoliths matched (96%) with their sectioned otoliths when compared directly for age 0- and age-1 fish, whole otoliths were used to age the young fish. Whole otoliths that had more than one annulus or that were questionable were sectioned and aged. The left otolith was used for age estimation unless it had been broken, lost, or damaged, in which case the right one was used.

Otoliths were embedded in Araldite resin and cured at 60 °C for 3 hrs. Individual otoliths were then hot-glued onto cutting paper, and three transverse sections were cut to approximately 0.5 mm thick using a multiblade low-speed saw. The sections were rinsed, dried, and mounted on a slide with Flo-Texx mounting medium. Annuli were counted using a dissecting microscope with either transmitted or reflected light. Two different readers estimated age independently for 200 otoliths. Percentage agreement, mean percentage error, and coefficient of variation (CV) between the ages determined by the two readers were calculated based on methods from Chang (1982). The two readers had 97.5% agreement, a mean percentage error of 0.48%, and a CV of 0.69%. Because of this high level of agreement between readers, one reader read all remaining otoliths twice on separate occasions. If the two independent readings did not agree, a third reading was done. If an agreement could not be reached, the otolith was eliminated from the analysis (n = 24).

In assigning an age to each fish, a biological birth date of April 1 was assumed based upon *C. proridens'* peak spawning period, determined by analysis of reproductive samples from our study (Murphy and Taylor 1989, Taylor et al. 2000, VanderKooy 2009). To match age with the year of birth, we adjusted the age based on the otolith
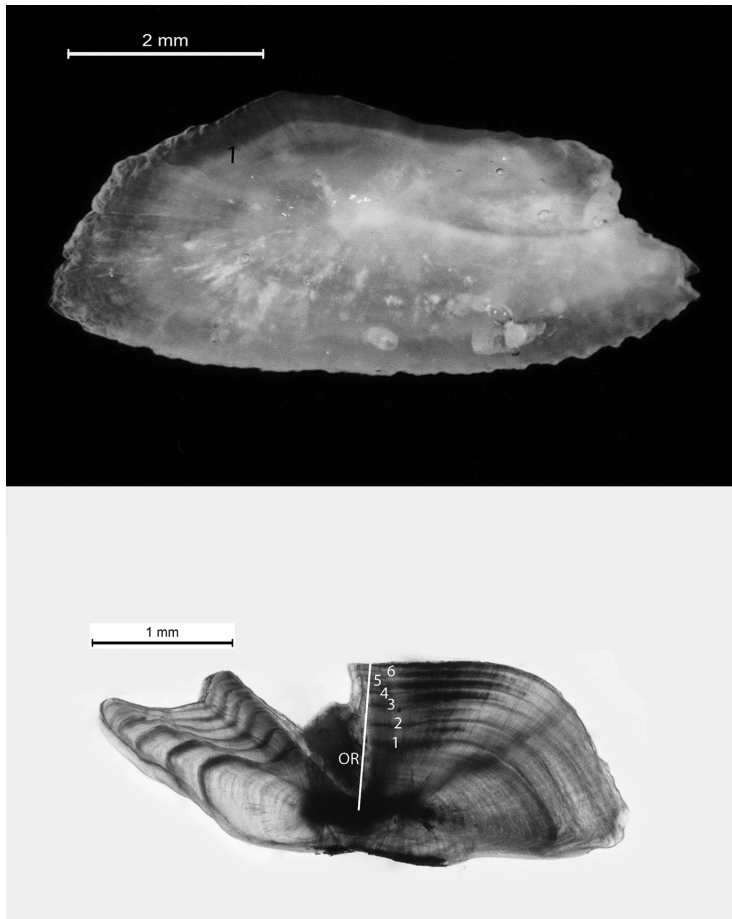
Figure 2. Whole otolith from an age-1 *Calamus proridens* (164 mm FL) (top) and a sectioned otolith from a 6-yr-old *C. proridens* (274 mm FL) (bottom); both samples were taken in November 2005. OR = otolith radius. Note the wide marginal increment subsequent to the sixth annulus.

margin. Each otolith was assigned a margin code ranging from 0 to 3, with 0 meaning no margin (i.e., the last opaque zone is on the edge) and a 3 having a large translucent margin. Fish collected from April 1 through July 31 with a margin code of 3 were assigned an age equal to the annulus count plus one. Otoliths with a margin code of 0 or 1 and collected from January 1 through March 31 were assigned an age equal to the annulus count minus one. Otherwise, fish age was equal to the annulus count.

Marginal increment (MI) analysis was used to validate the aging method for *C. proridens.* The MI is the distance from the proximal edge of the last visible opaque ring to the otolith's edge. The timing of opaque ring formation can be determined by examining the monthly mean MI and, if it displays one yearly cycle, it can be inferred that opaque ring formation is an annual event (Barbieri et al. 1994, Crabtree and Bullock 1998, Hood and Johnson 2000). Measurements were taken along the ventral ridge of the sulcal groove from the core to the distal edge of each annulus and to the otolith's edge (Fig. 2) using Image Pro image-analysis software. Otolith radius and opaque bands were marked only on sections with a defined core and on otoliths

for which the two independent reads agreed on increment count. MI was calculated as the distance between the last opaque zone and the otolith's edge, expressed as a fraction of the distance between the last and next-to-last opaque zone (Burgos et al. 2007). MI analysis was done on fish aged 1 to 9.

Gear selectivity was evident, trawls caught more smaller fish, while hook-and-line caught more larger fish; nevertheless, to get a complete size range of lengths and ages of *C. proridens,* we considered the length- and age-frequency distribution obtained from combined gears as the best estimate of *C. proridens* length and age composition for the GOM (Ricker 1975). While the Kolmogorov-Smirnov (KS) tests showed the age and length distributions were statistically different by gear, the observed range of ages collected by each gear was similar. Accordingly, data from all gears were combined to examine the overall life history of *C. proridens*; gears were still treated separately for regional comparison analyses.

The von Bertalanffy growth model (Ricker 1975) was fitted to observed length-at-age data using nonlinear regression with a Marquardt algorithm (PROC NLIN, SAS Institute Inc. 2006). The von Bertalanffy equation used to calculate growth was:

$$L_{(t)} = L_\infty \times (1 - e^{-k(t-t_0)})$$

where $L_{(t)}$ = the FL of the *i*th individual at age *t*, L_∞ = the asymptotic average maximum FL, k = Brody growth coefficient, t = age, and t_0 = the hypothetical age at which FL is 0 (Ricker 1975). Two separate von Bertalanffy analyses were conducted; one calculated growth using all the data combined and another one to specifically test for regional differences using only data from the trawl surveys. Regional comparisons used only the trawl data since the majority of the samples came from this gear, and this survey was the only one conducted in both regions. A randomization analysis was used to test if the null hypothesis that there is no difference in growth between the central and southern regions could be rejected (Manly 1991, Helser 1996). The randomization analysis generated an empirical distribution of the test statistic. We used 1000 iterations with the trawl data from the two regions to create the empirical distribution for the randomization analysis. For each iteration, each data point was randomly assigned to one of the two areas before calculating the test statistic. The test statistic, *t(x),* then represented the difference in the pooled data residual sum of squares (RSS) and the sum of the RSS generated for the two different regions [*t(x)*= pooled RSS − (RSS central + RSS southern)]. The probability of observing *t(x)* was then calculated by comparing *t(x)* to the generated empirical distribution. We considered the two curves to be significantly different if *t(x)* occurred in the tail of the distribution, i.e., the region beyond the significance threshold. We defined the significance value to be a probability <0.01, or a result of fewer than 10 outcomes out of 1000 exceeding *t(x)* (Manly 1991, Helser 1996).

Male and female length- and age-frequency distributions were compared using the KS two-sample test (Sokal and Rohlf 1981). Analysis of variance (ANOVA) and *t*-test analyses were used to compare differences in mean length and mean length at age by sex using the statistical software package STATISTICA (StatSoft 2005).

REPRODUCTION.—Sex was recorded in the field when possible by recognizable ovaries for females, testes for males, or by the presences of both ovaries and testes for transitional. Random subsets of gonads were collected for histological evaluation.

Gonads were removed and placed in 10% buffered formalin in the field. In the laboratory, gonads were rinsed, soaked in water for 1 hr, drained, and repeated. The two rinses were followed by a 12-hr soaking prior to being transferred to 70% ethanol. To evaluate any differences in the gonad tissue, anterior, middle, and posterior sections were removed from both lobes of 44 gonads and examined histologically. The analysis of the gonads from those samples revealed no difference in reproductive phase between lobes, so whichever lobe was in the best condition was used for histological evaluation. Gross observations of gonads undergoing sexual succession showed the configuration of germinal tissues to be of the delimited type, based on the Sadovy and Shapiro (1987) criteria for hermaphrodites. Connective tissue delimits the male tissue from female tissue and the male tissue begins growing posteriorly above the female tissue. At a minimum, the posterior section was used for histology. An additional section was occasionally taken on gonads that macroscopically had both male and female tissue for further evaluation of the transitional process. Preliminary archive samples of 100 female gonads only had a middle section taken; these gonad samples were staged based on the criteria for female reproductive phase. With only a middle section, the chance of not seeing the presence of male tissue increases, but male tissue was observed in 10 of those samples. Gonads were stained with hematoxylin-eosin (HandE) or periodic acid–Schiff's reagent, metanil yellow and hematoxylin (PAS/MY) (Quintero-Hunter et al. 1991). Females were assigned to a reproductive phase based on oocyte development criteria from Brown-Peterson et al. (2011). Transitional individuals were identified based on criteria from Sadovy and Shapiro (1987). If a specific reproductive phase could not be determined, gonads were categorized in general as immature, spawning, mature, or unknown. Males were classified as developing or mature (spawning capable).

The overall sex ratio was tested by 10 mm length intervals and by age for significant departure from a 1:1 ratio with χ^2 expectancy analysis. Logistic regression was used to estimate length and age at which 50% of the population underwent sex change from female to male (PROC LOGISTIC, SAS Institute Inc. 2006). The same methodology was used to estimate the length and age at which 50% of the females reached maturity. To prevent misclassification of regenerating (primary growth mature) specimens as immature, only females collected during the spawning season (February–May) were used in the logistic regression for determining maturity (Lowerre-Barbieri et al. 2011). Females were considered sexually mature if the gonad was assigned to the developing phase or one of the more advanced gonad phases.

Results

Sample Collection.—In total, 1814 *C. proridens* were collected and processed from the eastern GOM between 2000 and 2007. Fish from all months were represented in the data set, but the majority of fish were collected during the spring and fall. Fish were collected at depths from 9 to 60 m; small fish (<160 mm) were restricted to depths of <40 m, while larger individuals were captured at all depths.

Calamus proridens collected in the present study ranged in length from 76 to 361 mm (mean = 174 mm, SE 1.22, *n* = 1814). No significant differences between the length-weight relationship for males and females were found (ANCOVA; *n* = 1298, F = 0.05, *P* = 0.95), so all fish were pooled for analysis. Total weight (TW) ranged from 12.5 to 1115.0 g (mean = 146.8, SE 3.79, *n* = 1298). The linear relationship for

the log-transformed length-weight relationship was: $TWlog_{10} = 2.28 \times FLlog_{10} - 4.18$, $R^2 = 0.993$.

Age and Growth.—Otoliths from 1418 specimens were used for aging analysis: 1047 sectioned, and 371 whole. Consensus on age was reached for 1415 fish. *Calamus proridens* collected during the study ranged in age from 0 to 10 yrs, with the majority (88%) between ages 0 and 4 (Table 1). Only 14 fish (1%) were older than age 7. The largest individual was 361 mm (6 yrs old); the smallest specimen was 76 mm (age 0). The oldest specimens were 10 yrs old with lengths of 308 and 355 mm (collected on hook and line).

Marginal increment analysis was performed on 663 ototliths from ages 1 through 9 and revealed that annulus deposition occurred once a year during the spring and early summer (Fig. 3). Even though sample size was small for some months, the greatest difference in MI was between the lowest MI in April and the highest MI in October. The mean MI in April (mean = 0.30, SE 0.01) was significantly smaller than the mean marginal increment for October (mean = 0.69, SE 0.02) (*t*-test: $F = 1.34$, $t = -18.75$, $P = 0.04$). In April, MIs were either large (52%), indicating that an annulus was about to form, or small or right at the edge of the otolith (38%), indicating that the annulus had recently formed. For October and November combined, 85% had small MIs indicating that the annulus had already formed; no annuli were recorded to be on the edge.

The von Bertalanffy growth equation, fitted to all observed length at age data (all sexes and gears combined), was $L_{(t)} = 306 \times (1 - e^{-0.254(t + 1.69)})$ (Fig. 4A, Table 2). Length increased rapidly until age 2 (mean length = 193 mm), >50% of the total growth was completed by age 2, and growth slowed after age 2 (Table 1). Fish collected from the trawls ranged in age from 0 to 9 yrs for both the central and southern regions, and ranged in size from 99 to 322 mm in the central region and from 76 to 283 mm in the southern region (Table 3). Based on analyses of trawl data, the asymptotic length was greater in the central region than it was in the south; however, the rate (*k*) at which they reached the asymptotic length was similar between the regions (Fig. 4B, Table 2). The test statistic from the randomization analysis *t(x)* exceeded all 1000 randomized iteration values used to construct the empirical distribution [test statistic *t(x)* =
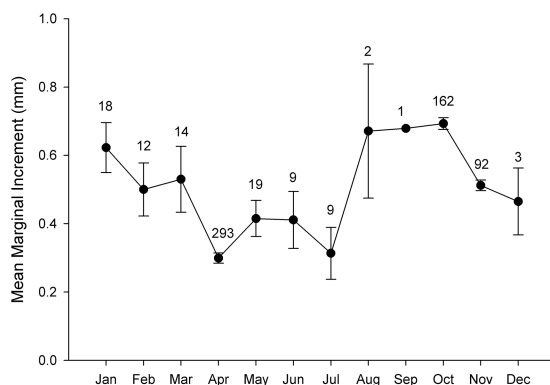

Figure 3. Mean marginal increment for *Calamus proridens* ages 1–9 yrs, *n* = 663, error bars = standard error. Numbers above error bars indicate sample size.

Table 1. Sample size, observed mean fork length (mm) at age (yrs), and range for *Calamus proridens* by sex and all samples combined (all includes samples that could not be sexed).

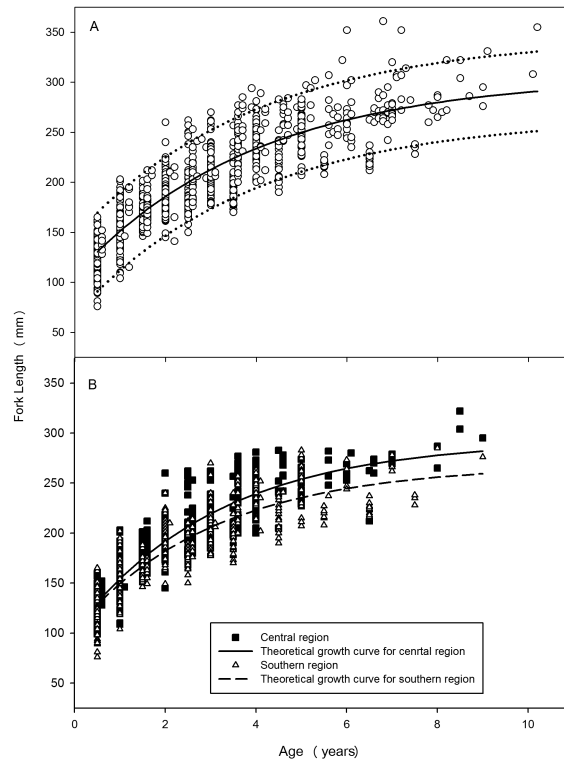| Age	Female			Male			Transitional			All		
	n	Mean (SE)	Range	*n*	Mean (SE)	Range	*n*	Mean (SE)	Range	*n*	Mean (SE)	Range
0	233	128 (1.00)	76–165				1	136	136	242	127 (0.97)	76–165
1	372	157 (0.83)	104–212	34	173 (2.86)	141–203	11	168 (5.13)	131–201	422	158 (0.83)	104–212
2	217	188 (1.07)	141–243	19	220 (4.65)	189–262	9	207 (7.59)	173–253	259	193 (1.26)	141–262
3	116	203 (1.90)	170–294	50	236 (2.82)	200–285	14	227 (6.36)	179–266	190	215 (1.86)	170–294
4	56	229 (2.88)	190–283	68	248 (1.86)	205–289	4	239 (15.57)	212–284	139	240 (1.78)	190–289
5	10	240 (8.21)	207–294	54	259 (2.93)	211–322	1	208	208	75	253 (2.79)	207–322
6	8	265 (7.63)	235–297	27	270 (6.22)	220–361				49	258 (4.56)	212–361
7				20	284 (5.23)	260–352	1	307	307	25	279 (5.47)	228–352
8				9	290 (7.11)	265–322				9	290 (7.11)	265–322
9				3	301 (16.13)	276–331				3	301 (16.13)	276–331
10				2	332 (23.50)	308–355				2	332 (23.50)	308–355

Figure 4. (A) von Bertalanffy growth model fitted to all observed fork length at age data for *Calamus proridens*; $L_{(t)} = 306 \times (1 - e^{-0.254(t+1.69)})$. Solid line = predicted growth curve; dotted lines = upper and lower 95% confidence intervals. (B) von Bertalanffy growth curves fitted to observed fork length at age, from trawl data only, for the central and southern regions of the eastern Gulf of Mexico; central: $L_{(t)} = 290 \times (1 - e^{-0.330(t+1.23)})$ southern: $L_{(t)} = 269 \times (1 - e^{-0.320(t+1.54)})$.

36,614, $P < 0.01$]. Accordingly, we rejected the null hypothesis that the two predicted mean-length-at-age growth curves from the central and southern regions were equivalent. The predicted lengths at age, for all fish combined, and the central and southern regions were similar to the observed mean length at age up to age 9; sample sizes were small for the older age groups (Table 3).

Table 2. Von Bertalanffy growth parameters, standard errors (SE), and 95% confidence intervals (CI) for all samples combined (all) and by region for *Calamus proridens* from the eastern Gulf of Mexico. n = sample size, Pred = predicted length.

Area	n	L_∞ Pred (SE)	L_∞ 95% CI Lower	L_∞ 95% CI Upper	k Pred (SE)	k 95% CI Lower	k 95% CI Upper	t_0 Pred (SE)	t_0 95% CI Lower	t_0 95% CI Upper
All	1,415	306 (5.72)	294.8	317.2	0.254 (0.015)	0.225	0.282	−1.69 (0.92)	−1.87	−1.51
Central	519	290 (6.82)	277.0	303.8	0.330 (0.026)	0.280	0.380	−1.23 (0.11)	−1.51	−1.07
Southern	754	269 (5.96)	256.8	280.2	0.320 (0.030)	0.270	0.371	−1.54 (0.12)	−1.78	−1.29

Table 3. Age, observed mean fork length (mm), and predicted mean for *Calamus proridens* by region for trawl data only and for all ages (yrs) and regions combined. Range in length for each age is also given for the central and southern regions. *n* = sample size.

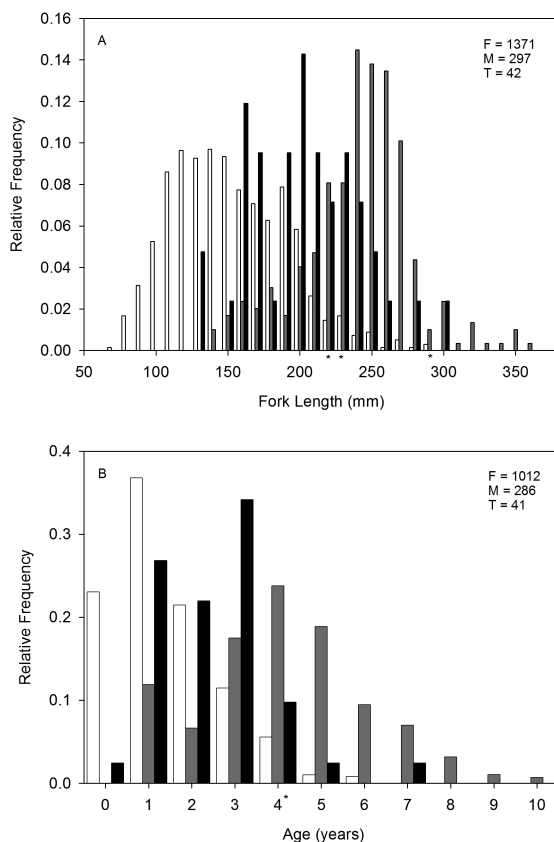| Age	Central				Southern				All		
	n	Mean (SE)	Range	Predicted mean	*n*	Mean (SE)	Range	Predicted mean	*n*	Mean (SE)	Predicted mean
0	77	126 (1.38)	99–160	129	131	126 (1.49)	76–165	129	242	127 (0.97)	130
1	152	162 (1.61)	109–212	160	259	155 (0.79)	104–202	154	422	158 (0.83)	157
2	110	200 (1.92)	145–262	198	136	186 (1.36)	149–240	188	259	193 (1.26)	192
3	80	219 (2.66)	185–277	224	100	208 (2.14)	170–270	211	190	215 (1.86)	219
4	64	241 (2.43)	200–281	241	58	233 (2.53)	190–263	226	139	240 (1.78)	237
5	17	255 (4.07)	229–282	255	43	245 (3.30)	207–283	236	75	253 (2.79)	252
6	9	259 (6.60)	212–280	266	17	231 (4.04)	215–273	247	49	258 (4.56)	267
7	5	276 (1.76)	270–279	271	8	256 (6.66)	228–278	252	25	279 (5.47)	274
8	4	295 (12.16)	265–322	278	1	285		256	9	290 (7.11)	281
9	1	295		281	1	276		259	3	301 (16.13)	286
10									2	332 (23.50)	291

Figure 5. (A) Length- and (B) age-relative frequency distributions of *Calamus proridens* collected from the eastern Gulf of Mexico, 2000–2007. White bars = females; dark gray bars = males; black bars = transitionals. Asterisks indicate sex ratios by length class and age that were not significantly different from the expected 1:1 ratio.

Reproduction.—Sex was determined for 1606 specimens: 80% were female; 17% were male; and 3% were transitional. Females ranged from 76 to 297 mm and were 0 to 6 yrs old (Fig. 5A, B, Table 1). The mean length for females was 156 mm, with a mean age of 1.4 yrs; 82% of females aged were between 0 and 2 yrs. Males ranged in length from 141 to 361 mm with a mean length of 244 mm (Table 1). The males ranged in age from 1 to 10 yrs, with a mean age of 4.2 yrs. More than half (58%) of the males aged were between 3 and 5 yrs old; only a few ($n = 14$) were older than 7 yrs (Table 1). The age and length distributions differed significantly between males and females (Fig. 5A, B). Males were significantly older and larger than females (age: KS Dmax = 0.627, $P < 0.01$; t-test $F = 2.41$, $t = -28.3$, $P < 0.001$; length: KS Dmax = 0.757, P < 0.01, t-test $F = 1.06$, $t = -35.2$, $P < 0.001$). In all ages that had observations for both sexes (ages 1–6) the mean length at age was significantly larger for males than females (ANOVA: $P < 0.01$) except at age 6. The overall sex ratio (1:4.6 males to females) was significantly different from the null hypothesis of a 1:1 ratio that is typical of gonochoristic fish ($\chi^2 = 691.5$, $P < 0.001$). Sex ratio by individual length and age class for males and females also had a significant deviation from the null hypothesis
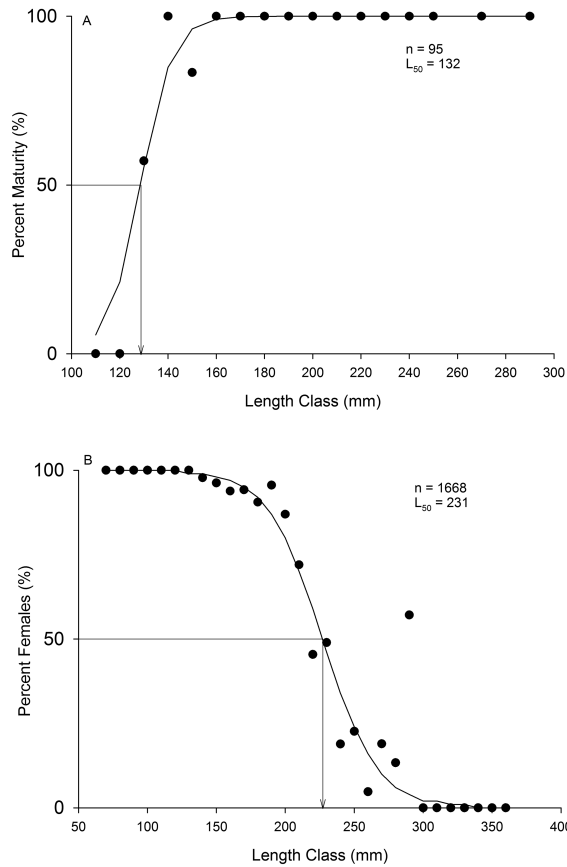
Figure 6. Percentage of (A) mature female and (B) female *Calamus proridens* by fork length showing a logistic function (continuous line) fitted to the observed data. Arrows indicate (panel A) predicted size at which 50% of the population was mature and (panel B) predicted fork length at which 50% percent of the females transitioned into males.

of a 1:1 for all length and age classes except length bins 220, 230, and 290 mm (Fig. 5A) and age 4 (Fig. 5B).

Calamus proridens matured at a small length and early age. Estimated length for females at 50% maturity was 132 (SE 2.25) mm, and maturity increased rapidly as length increased (Fig. 6A). The largest immature individual observed was 156 mm. The logistic regression indicated that 50% of the individuals mature during the first year (age 0) and that all probably are mature by the end of the second year (age 1–2).

A total of 388 gonads were processed for histology and were either ovarian, ovotestes (hermaphroditic females), transitional, testicular, or hermaphroditic males. Figure 7 shows macroscopic identification of ovarian (Fig. 7A), transitional (Fig. 7B), and testicular (Fig. 7C) gonads. Ovotestes—ovarian tissue with a small quantity of testicular tissue (male cyst) attached to the ovarian wall (Fig. 8F)—were observed in 39% of the gonads that had a complete ovarian wall. The testicular tissue of the ovotestes ranged in size and development; small and large cysts contained primarily spermatagonia, although some larger cysts exhibited ongoing spermatogenesis.
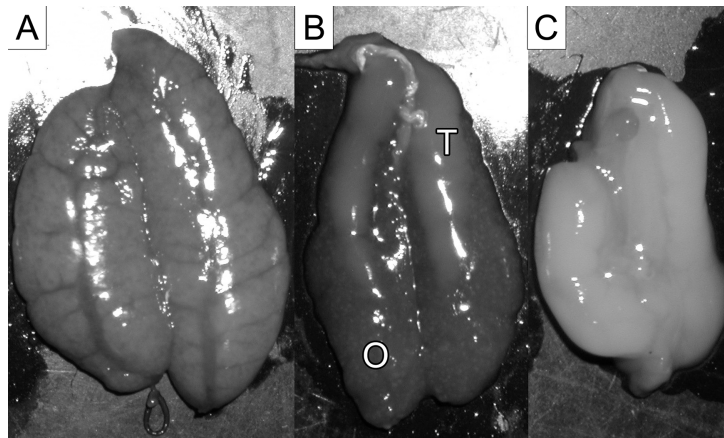
Figure 7. Macroscopic views of (A) ovarian, (B) transitional, and (C) testicular gonads from *Calamus proridens* collected in the Gulf of Mexico. O = ovarian tissue; T = testicular tissue.

The majority of the ovotestes were observed in October, November, and April, but they were also observed in January, July, and December. The specimens with testicular tissue undergoing spermatogenesis were larger and older (mean FL = 218 mm, mean age = 2.3 yrs) than the specimens with testicular tissue that only contained spermatogonia (mean FL = 165 mm, mean age = 1.1 yrs). Ovotestes containing only spermatogonia were observed in individuals as young as age 0, while ovotestes with spermatogenesis were not observed until age 1; both were observed up to age 4.

Histological evidence confirms that *C. proridens* is a monandric protogynous hermaphrodite, meaning that males only arise from sex change of females. Transitionals were determined by the presence of proliferating male tissue and degenerating female tissue (Fig. 8 A, B, C). In total, 42 transitionals were observed, 38 of them confirmed through histology. Females undergoing sex change ranged in length from 131 to 307 mm and in age from 0 to 7 yrs; however, the majority were observed between 1 and 5 yrs (Table 1). The mean length and age of females undergoing sex change were 207 mm and 2.4 yrs; with the majority (83%) of fish undergoing sex change between ages 1 and 3. The estimated age and length at which 50% of the population had transitioned from female to male were 4 yrs and 231 mm (Fig. 6B).

From histological gonad samples, transitionals were observed in January, April, July, October, and November, but gonad samples were not collected in all months, and the sample size was small for some months. Most (64%) transitionals were observed in the fall during the nonspawning season when the females were usually in the regenerating phase. Transitionals were also observed in the spring during the spawning season (26%). One transitional collected during the spawning season appeared to have equal amounts of male and female tissue in the same reproductive phase. The female tissue had hydrated oocytes and post-ovulatory follicles (POFs), and the male tissue was full of sperm. However, simultaneous hermaphroditism was unlikely (or at least ineffective), because the male did not have the means to disperse sperm: the vas deferens had not developed.

In total, 188 female gonads were examined for histological evaluation. All reproductive phases for female gonads were observed in the histological samples (*n* = 147). In cases when immature and regenerating gonads could not be distinguished, the gonads were classified as unknown (*n* = 41). Female gonads showed signs of spawning
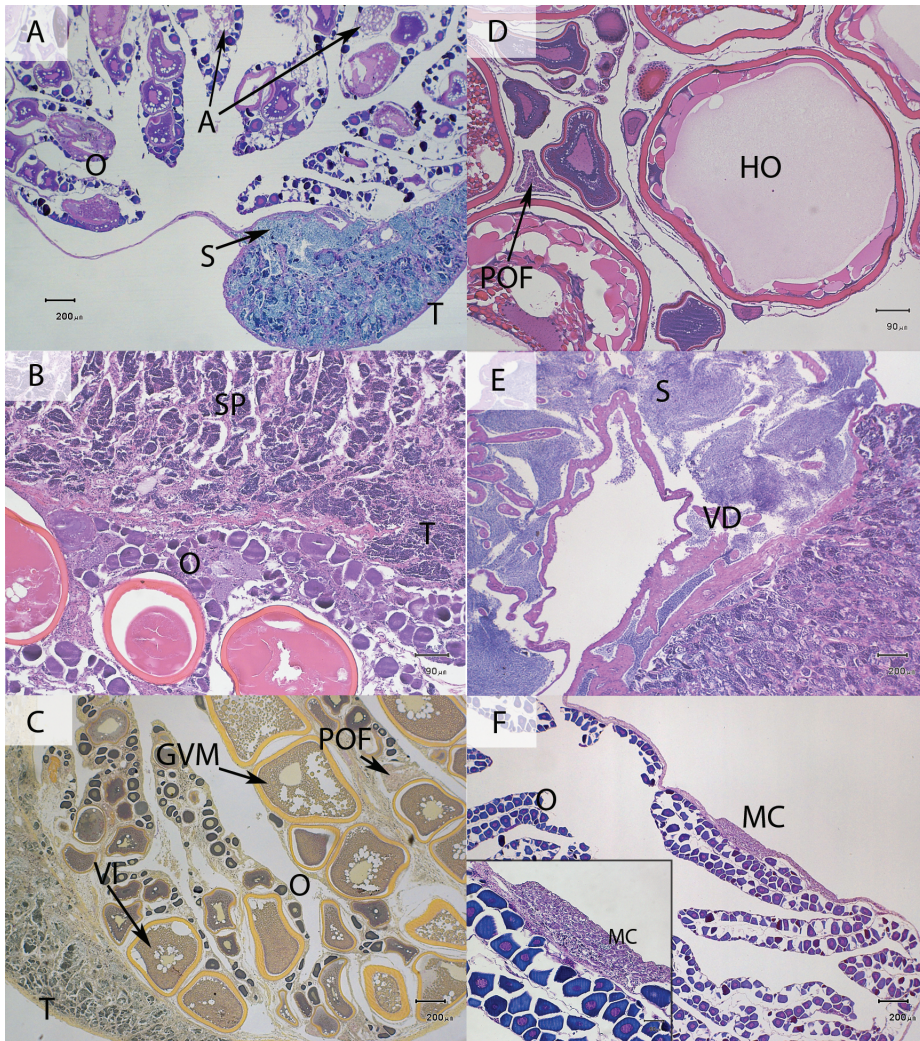
Figure 8. Histological gonad sections from *Calamus proridens*. Transitional gonad with prolif-erating male tissue and degenerating female tissue from a (A) 131 mm FL specimen collected in April 2007, (B) 167 mm FL specimen collected in April 2003, and (C) 225 mm FL specimen collected in April 2006; gonad of a (D) spawning female of 205 mm FL collected in April 2003, (E) spawning male of 216 mm FL collected in April 2004; (F) regenerating female gonad with a small male cyst from a 163 mm FL specimen collected in November 2005. T = testicular tissue, O = ovarian tissue, S = sperm, A = atretic oocyte, SP = spermatogenesis, VI = vitellogenic oocytes, GVM = germinal vesicle migration, POF = post-ovulatory follicle, HO = hydrated oocyte, VD = vas deferens, MC = male cyst.

from February through May (*n* = 60), and the few gonads observed in July were re-generating (no female gonads were collected in June, August, or September) and no immature female gonads were observed during this time. In April, 73% of the gonads were classified as spawning indicating their possible peak spawning period and selec-tion of April 1 for their biological birthdate. Spawning females ranged in length from 138 to 297 mm (mean = 200 mm, SE 3.74). *Calamus proridens* are batch spawners,

and 17 of 19 females with hydrated oocytes also had POFs, which suggests that they could be daily spawners (Fig. 8D). In the fall, only immature or regenerating phases were observed (n = 55).

In total, 136 males were collected for histological evaluation. Testes of hermaphroditic males (n = 38) had functional male tissue but traces of ovarian tissue as well. Timing of male reproduction was difficult to determine because the majority (89%) of male testes examined had sperm. Six male gonads had visible sperm ducts filled with sperm (Fig. 8E) and were classified as spawning males, while only nine testes had the presence of spermatogonia and spermatocytes and were most likely immature males.

Discussion

The present study is the first to determine age and reproductive biology of *C. proridens* in the GOM. While some basic life-history information has been reported on *C. proridens* from the Campeche Bank, Yucatán, ages were not determined and reproductive phase was not confirmed as they were in the present study for the eastern GOM population. The information on age, growth, seasonal reproduction, and timing of sex change can be used to further understand the reproductive biology of protogynous fishes in general, and *Calamus* species in particular.

Although there is no directed commercial fishery for *C. proridens,* they are a significant bycatch in the red snapper and shrimp fisheries and a major component in the nearshore/offshore reef fish assemblage. In addition, *C. proridens* are often caught in the recreational fishery, although they are not targeted as heavily as groupers, snappers, or red porgy. If restrictions continue to increase on other reef species, fishers may begin to target species on which there are fewer restrictions, such as *C. proridens*. Having data available on less targeted species will help monitor changes in fish assemblages and facilitate more accurate stock assessments, in addition to helping inform an ecosystem-based approach to monitoring and managing reef species in the GOM.

Age and Growth.—Otoliths are an accurate and valid method for aging *C. proridens.* Age-0 and age-1 fish could be accurately aged with whole otoliths, but the ability to discern annuli in whole otoliths decreases with age. Annuli in sectioned otoliths were easily identifiable, with distinct opaque bands. Of more than 1000 otoliths, only two had to be discarded due to reader disagreement on age, underscoring the ease in resolving annuli in sectioned otoliths of *C. proridens*. Scales have been used to age other *Calamus* spp., but not with the same accuracy as otoliths (Waltz et al. 1982, Horvath et al. 1990); therefore, sectioned otoliths should be the preferred method of aging *C. proridens*.

The MI analysis in the present study indicated that *C. proridens* deposited a new annulus during spring and summer (April–July), consistent with annual deposition. The marginal increment data showed variability in timing of annulus formation. The variability may be due to small sample sizes in some months, coupled with a protracted spawning period, causing formation of the opaque band to occur over a long period of time. Nonetheless, a significant difference in marginal increment was observed between April (smaller MI) and October (larger MI). Various other life-history studies on similar sparids of comparable size have also reported annular

deposition to occur around the same time (June–August) as *C. proridens* from our study. A life-history study on the congener, *Calamus nodosus* Randall and Caldwell, 1966 (knobbed porgy 273–544 TL), off North Carolina and South Carolina indicated that annulus deposition was initiated in June and July; however, their attempt to verify it through MI analysis was inconclusive (Horvath et al. 1990). *Calamus leucosteus* Jordan and Gilbert, 1885 (whitebone porgy, 54–407 mm FL) off the east coast of Florida and the Carolinas also reported annular deposition occurred in July (Waltz et al. 1982) and a study on *P. pagrus* (173–420 mm FL) from the eastern GOM verified by MI analysis that annular deposition occurred from June to August (Hood and Johnson 2000).

Calamus proridens in the GOM are moderately long-lived, with an observed maximum age of 10 yrs and an observed maximum length of 361 mm. *Calamus proridens* from the Campeche Bank had a similar maximum length (approximately 340 mm: type of length measurement unspecified; Dubovitsky 1977a,b), compared to *C. proridens* in the present study, but ages were not determined in the Campeche Bank study. Few studies have been conducted on age and growth in porgies, and of those *C. proridens* is most similar to *C. leucosteus* in age and length. *Calamus leucosteus* from the South Atlantic Bight had a maximum age of 12 yrs and a maximum length of 407 mm FL (Waltz et al. 1982). *Pagrus pagrus* and *C. nodosus* live longer (ages 18 and 17 yrs, respectively) and obtain a greater length (420 mm FL and 544 mm TL, respectively) than *C. proridens* (Horvath et al. 1990, Hood and Johnson 2000). *Calamus proridens* collected during our study grew rapidly during their first 2 yrs; specimens collected from the Campeche Bank by Dubovitsky (1977b) also showed rapid growth in the early years, but specific growth parameters were not reported.

The asymptotic average maximum length (L_∞) estimated from the von Bertalanffy growth model for all data combined appeared low based on the observed maximum length. The small sample size for larger and older fish could have contributed to the low estimates of L_∞ when all the data were combined. Similar findings of low L_∞ were found in *C. leucosteus* due to low numbers of older and larger fish (Waltz et al. 1982). Based on trawl data only, *C. proridens* collected in the southern region had similar growth coefficients but attained a smaller maximum length than fish in the central region. A few studies have shown growth differences on a small spatial scale. Regional growth differences of white grunt, *Haemulon plumieri* (Lacépède, 1801), along the Gulf coast of Florida were attributed to the species' habit of remaining near a home reef, resulting in a lack of large-scale movement throughout their life (Murie and Parkyn 2005). Buesa (1987) found that tropical demersal fishes with similar maximum lengths exhibited different growth rates, with opportunistic feeders growing faster than fishes solely dependent on fish as their main food source. Regional differences in length-at-age can also be due to differences in mortality rates rather than differences in growth rates. For example, gray snapper, *Lutjanus griseus* (Linnaeus, 1758), off south Florida were smaller and younger than those in north Florida, mainly due to the greater fishing pressure and higher mortality rates in south Florida (Burton 2001). Further research on environmental parameters and additional biological studies, such as diet composition and mortality estimates may help explain the differences observed.

Reproduction.—Female *C. proridens* in the eastern GOM reach maturity at a small size and young age. *Calamus proridens* reached 50% maturity at a size of 132

mm within their first year, making it very likely that all are mature by the end of their second year. Early maturation is found in other species of *Calamus*. Female *C. leucosteus* reached maturity at age 1; small females (179 mm FL) had hydrated eggs (Waltz et al. 1982). *Pagrus pagrus,* however, matures later (2–4 yrs) and at a greater length (192–212 mm FL) (Pajuelo and Lorenzo 1996, Kokokiris et al. 1999, Hood and Johnson 2000).

Reproductive biology has been described for many sparids and is complex; some species exhibit protandry, others protogyny and rudimentary hermaphroditism in addition to separate sexes (Alekseev 1982, 1983, Garratt 1986, Buxton and Garratt 1990). However, only two studies on *Calamus* reproductive biology have been published (Waltz et al. 1982, Horvath et al. 1990). The present study, and other reproductive studies on protogynous sparids (Huang et al. 1974, Garratt 1986, Buxton and Garratt 1990, Kokokiris et al. 1999), showed that the sex change process of the gonad was delimited, which is different from the transitional process in other protogynous families, such as Serranidae (Coleman 1981, Fischer and Petersen 1987, Shapiro 1987, Cochran and Grier 1991, Bullock et al. 1996, Thurman 2004), Labridae (Warner and Swearer 1991, Shapiro and Rasotto 1993), and Scaridae (Muñoz and Warner 2004), for which sex change is undelimited and cannot be seen without histological evaluation. In the present study, some gonads had both testicular and ovarian tissue that could be seen macroscopically and classified as transitional. However, most transitionals were collected when the female was in the regenerating phase and the transitional state could not be seen macroscopically, therefore histological evaluation is needed to adequately determine protogynous hermaphroditism in *Calamus* species.

Histological analyses in the present study showed *C. proridens* to be a monandric, sequential, protogynous hermaphrodite, according to the criteria of Sadovy and Shapiro (1987). Further supporting our hypothesis of protogynous hermaphroditism were the: significantly different sex-specific length and age distributions; absence of small males; and a highly skewed sex-ratio toward females in the smaller size classes (90% female for size class 70–180 mm FL; Tyler-Jedlund 2009), a result consistent with protogyny, other *Calamus* spp. and other sparids. The fact that no males were found in the smaller length classes and that they comprised 84% of the larger (size class 260–360 mm FL; age 7–10 yrs; Tyler-Jedlund 2009), older fish strongly suggests males arise only from sex change. Populations from the Campeche Bank also reported a female-skewed sex ratio, but were less skewed toward females (1:2.7; Dubovitsky 1977b) than the overall sex ratio from our study. *Calamus nodosus* collected off North Carolina and South Carolina did not have a female-skewed sex ratio (Horvath et al. 1990), but this could be due to the low numbers of small fish in that study. Sex ratio statistics were not reported along the Atlantic coast for *C. leucosteus*, but females accounted for about 80% of the smaller length classes and males for 70% of the larger length classes (Waltz et al. 1982).

When the mean FL at transition in the present study was converted to TL (242 mm TL based on the FL to TL regression found in the present study), it was similar to that of the Campeche Bank population (240 mm length, measurement unspecified; Dubovitsky 1977b). The mean length of transitionals was always greater than that of females at the same age, which may indicate that the larger females in each age group were the first to change sex; this has also been observed, or suggested, in other studies on protogynous sparids (Alekseev 1983). The mean length-at-age of males was larger than that of females, which could indicate a possible growth spurt after

transition. The quantity of energy that goes into reproducing and changing sex could contribute to new growth in males after the transition is complete.

Many investigators have tried to explain the biological reasons for the existence of hermaphroditism, but no theory fits all sex-changing species. The implications for sex change in sparids are unclear. In some protogynous species, such as groupers and wrasses, a complex social mating structure regulates sex change (Fischer and Petersen 1987, Warner and Swearer 1991). The mating systems in sparids appear to be equally complex, though they have received only moderate attention. Buxton and Garratt (1990) described three types of mating behaviors in three sparid species: demersal spawning, pair spawning, and spawning in dense aggregations of individuals of similar size. Dubovitsky (1977a) suggested that *C. proridens* are sequential spawners that have different spawning grounds for different groups and indicated that they do not form dense spawning aggregations.

The sex ratio and size ratio threshold hypothesis combined with the density-dependent hypothesis could explain induction of sex change in *C. proridens*. The sex and size ratio models suggest that females may be induced to change sex (in the presence of a male) when a threshold number of females is reached or a threshold ratio of small to large individuals is reached for a given female (Ross et al. 1983, Shapiro 1987, Lutnesky 1994). For example, in the size-ratio model, Ross et al. (1983) showed that in the saddleback wrasse, *Thalassoma duperrey* (Quoy and Gaimard, 1824), sex change was stimulated by the presence of at least one other smaller fish and did not require removal of the male or largest fish. The theory is that if there is a skewed ratio toward larger fish (mainly males) and few smaller fish (mainly females) there are too few females for a new male to mate with and too many large males to compete with (Ross et al. 1983). However, if the ratio of smaller to larger fish is reversed and there are few larger fish, it may be reproductively advantageous to change sex. The sex-ratio model is similar in that there are a certain number of interactions a female is used to having with a male, and once that interaction rate is changed (decreased with an increase in the number of females), the female will change sex. In addition, different densities can induce sex change depending on the encounters assumed to be important in the sex change process. The latter model is similar to the sex- and size-ratio models except that it incorporates fish density and its effects on behaviors and simple proximity (Lutnesky 1994). Preliminary observations of the trawl data showed that all large trawl catches that included transitional fish had a high proportion of females to males. Therefore, sex change in *C. proridens* may not be as much about between-sex interactions as it is about interactions between individuals of the same sex. More detailed field or experimental studies on mating behaviors are needed to better understand the reasons for sex change in *C. proridens.*

Conclusions

Calamus proridens is a monandric, sequential, protogynous hermaphrodite. Histological examination of gonads in transition, the absence of small males, a highly skewed sex ratio toward females, as well as significantly different length and age distributions for males and females are consistent with our hypothesis of protogynous hermaphroditism. The fact that no males were found in the smaller length classes and that there were proportionately more males in the larger lengths and older ages strongly suggest that males arise only from sex change. The factors contributing to

the induction of sex change in *C. proridens* are still unknown. However, the cues for transition may be due to interactions within the same sex, rather than reaching a critical specific size or age. The wide range of size and age in transitionals points to a combination strategy, incorporating a sex and size ratio threshold combined with a density-dependent behavioral component (Ross et al. 1983, Shapiro 1987, Lutnesky 1994). The mating system of *C. proridens* is currently undescribed.

Life-history information for most porgies is quite limited. The present research provides life-history information on age, growth, reproduction, and sex change that can be included in stock assessment models and thereby improve the management of fisheries resources in the GOM, especially as management progresses from single-species to ecosystem-level approaches. Models for gonochoristic species are not appropriate for hermaphroditic species (Brooks et al. 2008). When lacking species-specific information on sex change, the information from our study may be incorporated to improve the stock assessments of similar hermaphroditic species. Hermaphroditic species respond differently than gonochoristic species to overfishing (Crabtree and Bullock 1998, Alonzo and Mangel 2004). Size-selective fishing pressure on a hermaphroditic species can seriously impact the overall dynamics of the population and timing of sex change (Alonzo and Mangel 2004). For example, removal of larger males will further skew the sex ratio toward females; this in turn can affect overall spawning success and can result in a smaller size of transition (Crabtree and Bullock 1998, Hood and Johnson 2000, Alonzo and Mangel 2004). Stock management for sex-changing fish species will require consideration of behavioral and biological variables. Incorporating variables such as the mating system, sex ratios, social interactions, life-history strategies, and fecundity and fertility into stock assessment models will further increase the ability to understand the stock dynamics and predict the success of management strategies (Alonzo and Mangel 2004).

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