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Age, Growth, and Reproduction of Calamus proridens the Littlehead Porgy, from the Northeast Gulf of Mexico

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Age, Growth, and Reproduction of *Calamus proridens* the Littlehead Porgy, from the

Northeast Gulf of Mexico

by

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ABSTRACT

A total of 1814 *Calamus proridens* ranging from 76 mm – 361mm fork length (FL) were collected and processed along the central and northwest coasts of Florida between 2000 and 2007 to determine size, sex, age, and reproductive condition. Females ranged from 76-297 mm FL (mean FL=156 mm, n=1420), males ranged from 141-361 mm FL (mean FL=244 mm, n=297), and transitionals ranged from 131-307 mm FL (mean FL=207 mm, n=42). Sex ratios sorted by length class, age, and overall were significantly different from the 1:1 ratio for gonochoristic species (P<0.0001). Sagittal otoliths (sectioned and whole) from 1438 *C. proridens* were used to determine age. Marginal increment analysis suggested that a single annulus is formed each year in the spring. Ages ranged from 0 to 10 years with 88% of the fish being between 0 and 4 years. Females ranged in age between 0 and 6 years, while males ranged between 1 and 10 years. Growth was rapid in the first two years and then began to slow down. The von Bertalanffy growth model fitted to all observed data was $L_{(t)}=306[1-e^{-0.254(t+1.69)}]$. The data were further broken down into central and southern strata and the von Bertalanffy growth model showed that fish in the central region grow larger than those in the southern region. Histological analysis confirmed that *C. proridens* are protogynous

hermaphrodites with delimited type gonads. Estimates indicated that 50% of the females in the sample had transitioned into males by age 4 and a FL of 231 mm. *Calamus proridens* mature at a small size; 50% of the samples were mature by 132 mm and within the first year. The samples obtained indicated that the peak spawning season is in the spring. The presence of hydrated oocytes and post ovulatory follicles in the same ovary suggests that they are multiple spawners.

Introduction

The littlehead porgy (*Calamus proridens*) occurs in the Atlantic Ocean and Gulf of Mexico (GOM) from Florida to Louisiana, the Campeche Bank, and through the Greater Antilles (Darcy, 1986, Dubovitsky, 1977a, Pierce and Mahmoudi, 2001, Randall and Caldwell, 1966). Their distribution is influenced by salinity, temperature, water depth, and habitat structure, as well as; species and life history characteristics (Darcy, 1986). They are typically found associated with natural or artificial reefs, offshore platforms, and live bottoms consisting of sponges and corals (Darcy, 1986, Pierce and Mahmoudi, 2001). *Calamus proridens* have not been found in estuaries or in waters where salinity is less than 30 ppt (Darcy, 1986). Adults in the GOM are distributed from shallow near shore waters to depths as great as 60 meters (Darcy, 1986).

Calamus proridens is an important component of the nearshore/offshore fish assemblage of the west coast of Florida, and subtropical and tropical American waters in general (Darcy, 1986, Pierce and Mahmoudi, 2001, Randall and Caldwell, 1966). For example, *Calamus* proridens has been reported to be the most important and abundant member of the family Sparidae in the commercial fishery in the Campeche Bank, Yucatan. In the 1960s and 1970s research vessels collected over 500 kg per haul (Dubovitsky, 1977a).   They are often incidentally harvested by the commercial reef fishery in Florida (Darcy, 1986, Dubovitsky, 1977a, Randall and Caldwell, 1966). The red snapper (*Lutjanus campechanus*) commercial fishery harvested over 1.72 million pounds between 2002 and 2006 along the Florida west coast (personal communication

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from the Fish and Wildlife Research Institute) indicating that numerous porgies were probably also harvested even though no specific numbers are reported. Recreational harvest of porgies between 2002 and 2006 (not including pinfish, red porgy, or sheepshead) totaled over 67,000 kg from the Atlantic and Gulf coasts (personal communication from the National Marine Fisheries Service).

Even though *C. proridens* have a commercial and recreational importance, specific life history information is not well known, especially in the GOM. Randall and Caldwell (1966) did a diagnostic description on four new species of Sparids, including *C. proridens.* In the 1970s Dubovitsky reported life history characteristics for the Campeche Bank region, however his studies were based on length frequency analysis and the data do not specify which length was used (Standard Length-SL, Fork Length-FL, or Total Length-TL) in the analysis. Darcy (1986) did a biological synopsis on *C. proridens* and *C. arctifrons* with most of the findings paraphrased from Dubovitsky's studies.

Many species in the family Sparidae have been reported to be protandrous (male to female) (Besseau and Brusle-Sicard, 1995, Buxton and Garratt, 1990, Lee *et al.*, 2008) or protogynous (female to male) (Buxton and Garratt, 1990, Garratt, 1986, Haung *et al.*, 1974, Kokokiris *et al.*, 1999) hermaphrodites. Most research on sex-changing fish involves species within the families Serranidae (groupers and seabasses), (Bullock *et al.*, 1996, Cochran and Grier, 1991, Coleman, 1981, Fischer and Petersen, 1987, Shapiro, 1987, Thurman, 2004), Labridae (wrasses), (Shapiro and Rasotto, 1993, Warner and Swearer, 1991) and Scaridae (parrotfish) (Munoz and Warner, 2004). The sex reversal in those families is undelimited, where the male and female tissues are intermixed or separated within the gonad during the course of sex reversal. Little research has been

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conducted on the sex-changing processes of sparids, which are delimited (male and female gonads are separated by connective tissue) and most work has been done on South African species (Besseau and Brusle-Sicard, 1995, Buxton and Garratt, 1990, Garratt, 1986, Haung *et al.*, 1974, Lee *et al.*, 2008) or the red porgy (*Pagrus pagrus*) (DeVries, 2006, Hood and Johnson, 2000, Kokokiris *et al.*, 1999, Kokokiris *et al.*, 2006, Pajuelo and Lorenzo, 1996).

Disturbingly, fish populations are being depleted from overfishing (Alonzo, 2003, DeVries, 2006). The Magnuson-Stevens Act was reauthorized in 2006 with the goal of continuing to protect commercial and recreational fish communities as global fishery resources provide tremendous economical and ecological value. As the more highly valued fish become depleted and more highly regulated, commercial and recreational fishermen typically switch to more abundant species that are not as highly monitored (DeVries 2006).

Past stock assessment models were limited by the data that were available, however, they are now beginning to include life-history parameters such as mating behaviors, reproductive patterns, survival, and recruitment (Alonzo, 2003). Sex-changing fish add another level of complexity to stock assessment models that can have a large impact on their results and subsequent management decisions (Alonzo, 2003, Armsworth, 2001, Davis and Berkson, 2005). A better understanding of the protogynous life history strategy can benefit modeling efforts and our understanding of the sensitivity of protogynous species to overfishing (DeVries, 2006). Unlike dioecious (separate sexes) species, a size selective fishery on sex-changing fish can negatively impact reproductive rates and reduce population size to very low levels (Alonzo, 2003, Armsworth, 2001,

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Davis and Berkson, 2005). Including life history information in stock assessments will further our understanding of those species' vulnerability to exploitation, and may help eliminate future fish populations from fishing moratoria or population crashes.

Calamus proridens are suggested to be monandric (arising only from sex change) protogynous hermaphrodites (female to male) whose growth rates may be both age- and sex-dependent. However, there is little information on age and size of the transition period and reports have come only from the Campeche Bank. Hermaphroditic fishes are especially vulnerable to exploitation, as fisheries typically target the largest fishes first. This practice tends to remove the largest fishes from the system and disrupts the reproductive ability of the population (Alonzo, 2003, Armsworth, 2001, Crabtree and Bullock, 1998, Davis and Berkson, 2005). Precise, timely information describing size at age and sex and age at sex-reversal will allow an accurate assessment of *C. proridens* stocks and provide detailed information for the GOM. Including new information from a single-species study into a multi-species model will allow further development for an ecosystem-based approach to managing fisheries resources in the GOM.

The main objectives of the present research were to describe the age and growth, and reproductive behavior of *Calamus proridens* from the northeast Gulf of Mexico concentrating on age and size at sexual transition.

Materials and Methods

Geographic coverage

The majority of the samples were obtained in the spring (April and May) and fall (October and November) from 2003-2007 during the Fisheries-Independent Monitoring (FIM) programs' baitfish surveys aboard the *R/V Tommy Monro*. Samples were collected using a 65-ft balloon trawl that was towed for 30 minutes per sample. Spring surveys were conducted between 2003 and 2007 and the fall surveys between 2004 and 2006. Samples were collected at randomly selected sites off the central west coast of Florida between the 28° N and 26° N (Fig. 1). Samples were also obtained from the FIM gear-testing cruises in October 2006 and July 2007 aboard the *R/V Suncoaster* and *R/V Bellows*, using baited Chevron traps with 60 minute soak times. The October 2006 cruise collected samples between 27° 48' N and 27° 26' N; the July 2007 cruise collections were from the Florida middle grounds between 28° 50' N and 28° 20' N. Additional samples were collected from the Fisheries-Dependent Monitoring (FDM) program, the National Marine Fisheries (NMFS) archive database from Panama City, and recreational fishermen; all additional fishes were caught using hook and line.

Sample Collection

Standard, fork, and total lengths (mm) were recorded from samples taken on the baitfish survey. General linear regression was used to determine length to length relationships (over 1500 fish were used) and had R^2 values of 0.99 for all length combinations (Table 1). Those models were then used to obtain missing lengths from other samples. All
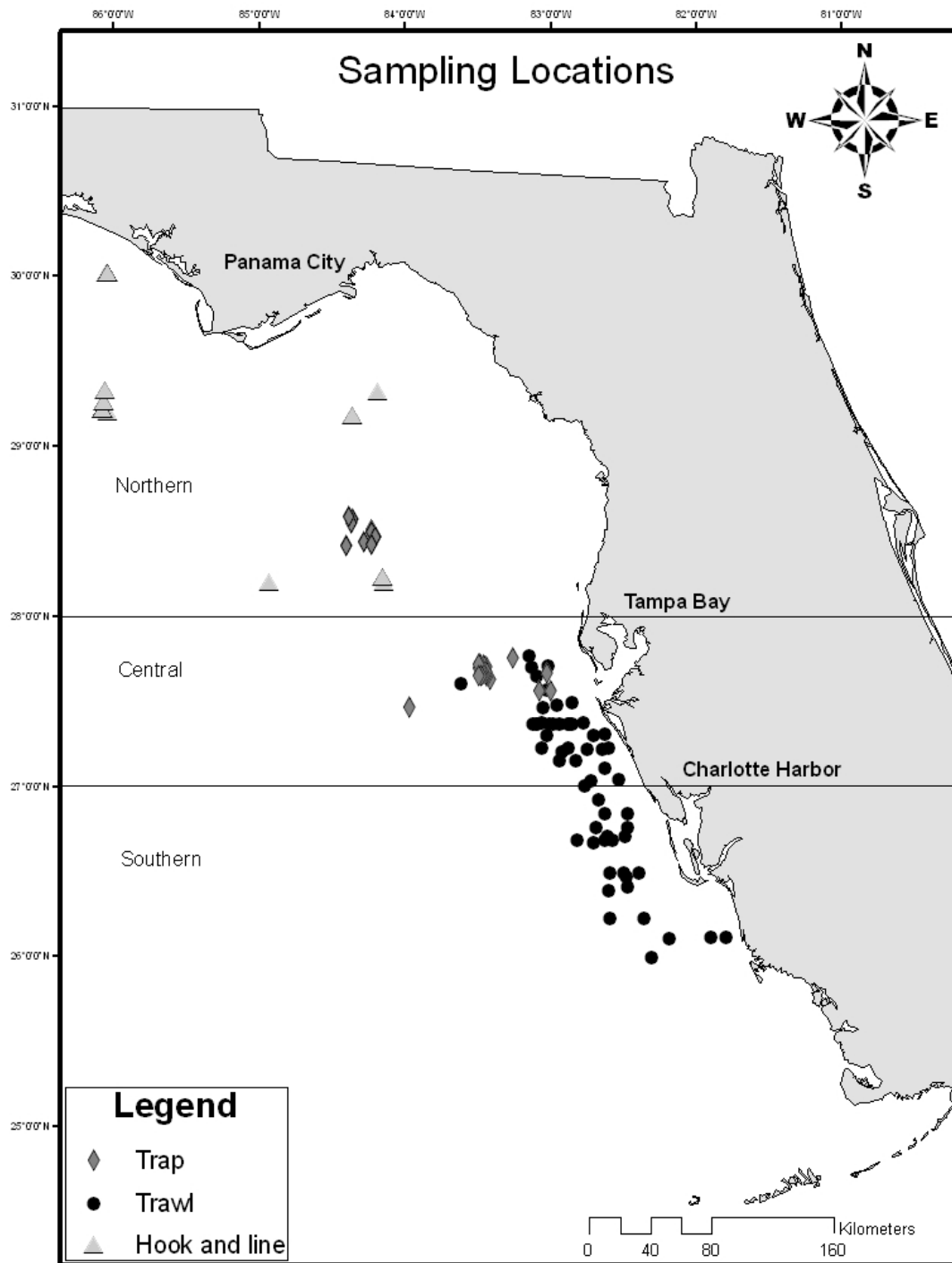
Figure 1. Sampling locations of *Calamus proridens* from the Fisheries-Independent Monitoring (FIM) program's baitfish cruise surveys (○), FIM gear testing cruises (◇), and samples collected from the National Marine Fisheries (NMFS) in Panama City from 2000-2007. Samples collected by FDM and recreational fisherman did not have latitude and longitude coordinates and are not represented in the map, but were collected in the Tampa Bay area.

Table 1. Relationship between standard, fork, and total length, and fork length and total weight of *Calamus proridens* from the northeast GOM. SL = standard length (mm), FL = fork length (mm), TL = total length (mm), WT = total weight (g). The fork length range for all length-length regressions was 76 – 361 mm and the total length range was 90 – 421 mm. Total weight range for length-weight regression was 12.5 – 1115 g.

Y	X	Y=ax+b			
		N	a	b	R^2
SL	FL	1545	0.88	-0.54	0.997
FL	SL	1545	1.13	1.21	0.997
SL	TL	1532	0.77	-4.31	0.992
TL	SL	1532	1.29	7.05	0.992
FL	TL	1558	0.87	-4.25	0.995
TL	FL	1558	1.14	5.93	0.995
WT_{log10}	FL_{log10}	1298	2.82	-4.18	0.993

Fork length- weight power equation

$$WT=7e^{-05}FL^{2.82}$$

results are reported based on fork length (FL) measurements unless otherwise noted.

Total weight in grams was recorded when possible. Frozen weights were taken in the lab

when fresh weights could not be obtained in the field. Fresh and frozen weights were

combined for length-weight analysis. Length and weight were log transformed and an

Analysis of Covariance (ANCOVA) was used to test for differences between sexes

(Froese, 2006, Ricker, 1975, Sokal and Rohlf, 1981). Location and depth (meters) were

recorded from the baitfish survey, gear testing cruises, and NMFS samples. Surface

salinity and temperature were recorded from the baitfish surveys but only salinity was

recorded from the NMFS samples.

Age and Growth

Fish age has been determined using calcified structures such as fin rays, scales

and otoliths (Ihde and Chittenden, 2003, Pannella, 1974). Otoliths are usually the

clearest and most accurate age markers when compared to other calcified structures

(Chambers and Miller, 1995). Depending on the species, age assessment can be done

with whole or sectioned otoliths (Gettel *et al.*, 1997, Thurman, 2004). In this study, fish

were aged using sectioned and whole sagittal otoliths (Fig. 2). Readability of large whole
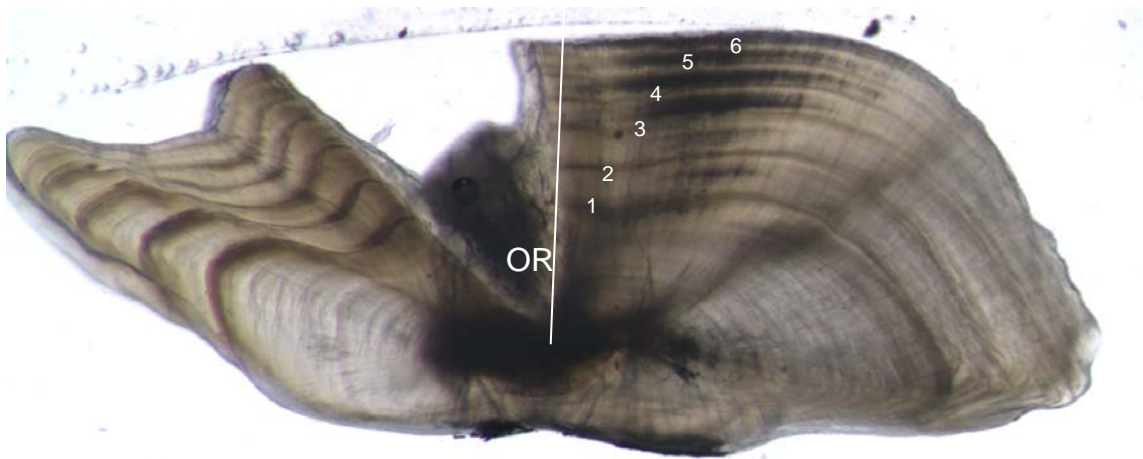
Figure 2. Whole otolith from an age one *Calamus proridens* (164 mm FL) (top) and a sectioned otolith from a six year old *C. proridens* (274 mm FL) (bottom), both samples were captured in November 2005. OR= otolith radius. Note the wide marginal increment subsequent to the sixth annulus.

otoliths can be affected due to clouding and crowding of rings, therefore, 202 otoliths were aged whole and then sectioned to identify the limits of aging using whole otoliths. Since there was a 96% agreement on whole versus sectioned otoliths for ages zero and one, all otoliths were aged whole first and then any whole otoliths with more than one annulus were sectioned and aged. Any questionable whole otoliths were also sectioned. The left otolith was used for age estimation unless it had been broken, lost, or damaged, in which case the right one was substituted.

Otoliths were embedded in Araldite resin and cured at 60°C for three hours. The otolith was then hot-glued onto cutting paper, and three transverse sections were cut to approximately 0.5 mm thick using a multi-bladed 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 reflective light. All otoliths were enumerated twice, independent of each other. In cases where the two independent reads did not agree, a third read was done. If an agreement could not be reached, the otolith was not used in analysis. To assign an age to each fish a birth date of April 1st was assumed based upon *C. proridens* peak spawning period. A margin code was also recorded with a range of 0 – 3, with 0 having no margin (i.e. the last annulus is on the edge) and 3 a large margin. Samples collected from April 1st to July 31st with a margin code of 3 were assigned an age equal to the annulus count plus one. Samples with a margin code of 0 or 1 and collected during January 1st through March 31st, were assigned an age equal to the annulus count minus one. Otherwise, fish age was equal to annulus count.

To evaluate growth, observed lengths at age were fitted to the von Bertalanffy growth model (Ricker, 1975) by using nonlinear regression techniques with a Marquardt algorithm (PROC NLIN; SAS 1996). The original von Bertalanffy equation used to calculate growth was:

$$L_{(t)} = L_\infty{}^*(1\text{-}e^{-k(t\text{-}to)})$$

where $L_{(t)}$ = the fork length of the *i* th individual at age *t*;
  L_∞ = the asymptotic maximum fork length;
  k = Brody growth coefficient;
  t = age;
  and
  t_0 = the hypothetical age at which fork length is zero.

Due to large variability in the model when all length and age data was combined from all areas; I separated the data into three regions based on latitude (Fig 1). There were not enough samples in the northern region to construct a growth curve. The central region was broken into two strata: a central (27° latitude) and a southern (26° latitude) to determine if growth differed by latitude. A randomization analysis of 1,000 iterations was used to determine if there was a significant difference between the central and southern strata (Manly, 1991).

The Akaike's Information Criteria (AIC) was used to measure the goodness of fit of the von Bertalanffy model to the data based on location. The smaller the AIC number the better the data fits to the model. The formula for the AIC was:

$$AIC=n^*log(RSS/n)+2^*P$$

Where n=sample size
  RSS= residual sum of squares from the growth model
  P = number of parameters in the model

Observed ages at length were used to construct an estimated size at age key (Ricker, 1975). Aged fish were assigned to 20 mm FL intervals and calculated age

distribution (as a percentage) for each size interval.

Age validation

Since age estimates had not been previously done on *C. proridens,* annual deposition of opaque rings was validated using marginal increment analysis. The marginal increment is the distance from the proximal edge of the last visible opaque ring to the otoliths edge. The timing of opaque ring formation can be determined by examining the monthly mean marginal increment. If the mean marginal increment displays a yearly cycle, it can be inferred that opaque ring formation is a yearly 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 otoliths edge (Fig. 2) using Image Pro image analysis software. Otolith radius and opaque bands were only marked on core sections and on samples where the two independent reads agreed on increment count. Since the distance from the core to the first annulus is usually the largest, the marginal increment was calculated using a proportion equation:

$$MI = \frac{OR - I_L}{I_L - I_{L-1}}$$

where   OR = otolith radius

I_L = distance from otolith core to last increment

I_{L-1} = distance from otolith core and the next to last increment

Back-calculation

Back-calculation is a technique used to infer a length from an earlier time based on a known length and age (Francis, 1990). Annuli measurements with fish length are used to estimate fish length at time of annulus formation. Back-calculation is often used

to help develop an age-length model to determine lengths of fish at ages that are rarely

caught. The biological intercept method from Campana (1990), which assumes a linear

relationship between otolith length and fish length and uses a biological intercept rather

than a statistical one, was used to back-calculate fork length at annulus formation:

$$L_a = L_c + (O_a - O_c)(L_c - L_i)(O_c - O_i)^{-1} ,$$

where L_i and O_i = fish and otolith length at biological intercept

L_c and O_c = fish and otolith length at capture

L_a and O_a = fish and otolith length at age

The biological intercept was calculated as the mean fish length and otolith radius of all

age 0 fish. To detect Lee's phenomenon that back-calculated lengths decrease with

increasing age a linear regression analysis was used to detect any trends (Francis, 1990,

Gotelli and Ellison, 2004, Schirripa, 2002, Sokal and Rohlf, 1981).

Reproduction

Gonad samples from various size ranges were collected for histological

evaluations. In the field, gonads were removed and placed in 10% buffered formalin.

Later, the gonads were rinsed and soaked in water for two one-hour periods, followed by

a final 12-hour soaking prior to being transferred to 70% ethanol. To evaluate variability

in the gonad tissue a subsample (n = 44) of all the gonads had an anterior, middle, and

posterior section taken from both lobes. Preliminary results indicated that there was no

difference in the reproductive class between lobes. Therefore, the lobe that was in the

best condition was used.   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 of hermaphrodites. Connective tissue delimits the

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male tissue from female tissue and the male tissue begins growing posteriorly above the female tissue. This result was confirmed macro- and microscopically. Therefore, at a minimum, the posterior section was used for histology. An additional section was occasionally taken for further evaluation of the transitional process. In 100 samples, only a middle section was obtained; those were staged and analyzed as far as possible. Samples were stained with Hematoxylin-Eosin (H&E). A few samples were also stained with Periodic Acid-Schiff's reagent Matalin Yellow (PAS/MY).   Females were assigned a reproductive class based on oocyte development criteria from Brown-Peterson et al. (2007) (Table 2). Transitionals were identified based on criteria from Sadovy and Shapiro (1987) (Table 2). When exact reproductive class could not be determined, samples were categorized as immature, spawning, mature, or unknown. Males were classified as immature (developing) or mature (spawning capable). The overall sex ratio for the entire sample, by 10 mm size intervals, and by age were tested for significant differences from a 1:1 ratio with chi-square expectancy analysis. I estimated length and age at which 50% of the population underwent sex reversal from female to male by fitting the observed data with a logistic regression (proc logistic; SAS). The same method was used to estimate the size and age at which 50% of the population reached maturity. To prevent misclassifying of regenerating (primary growth mature) specimens as immature, only samples collected in the spawning season were used for analysis. Females were considered sexually mature if the gonad was assigned to the developing class or the more advanced gonad classes.

Table 2. Histological criteria to assess reproductive classes for female *Calamus proridens*.

Female Class	Description
Immature	Only oogonia and primary growth present – no atresia, no signs of previous spawning
Developing (Cortical avelio)	Primary growth, cortical avelio and/or early vitellogenesis. No POF's
Spawning Capable (Vitellogenic)	Vitellogenic (VI) – may have primary growth and cortical avelio. Partially and fully yolked oocytes. Early VI with evidence of POF's
Actively Spawning (Final oocyte maturation)	Ovulating (within 12 hours), germinal vesical migration (GVM), hydrated oocytes, POF's, advanced yolk coalescence and breakdown of nuclear membrane
Regressing	Atresia – VI undergoing alpha and beta atresia – less developed oocytes often Present, possible POF
Regenerating (Primary growth mature)	Only primary growth present, muscle Bundles, enlarged blood vessels May not be able to determine from immature.
Transitionals	Proliferating male tissue, spermatocytes Spermatid, spermatozoa. Some atresia in females. Immature females, mainly only primary growth present.

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

Results

Sample Collection

A total of 1814 *C. proridens were* collected and processed from the Gulf of Mexico between 2000 and 2007. Samples were collected from all months, with the majority collected in the spring and fall. During the spring and fall baitfish surveys, samples were collected in waters with salinities ranging from 33.7 to 37.8 ppt and at temperatures between 19.4°C and 28.9°C. *Calamus proridens* from the northeast GOM were collected in temperatures ranging from 16.0°C to 24.8°C. Fish were collected at depths between nine and 60 meters. Fish less than 160 mm were only collected in depths less than 40 m, while larger fish were distributed among the whole range (Fig. 3).

The *C. proridens* used in the present study ranged in length from 76 to 361 mm (mean=174 mm, SD=52, n=1814) (Fig. 4). The total weight range for individuals was 12.5-1115 g (mean=146.8, SD 136.6, n=1298). The relationships between SL, FL, and TL, and FL to total weight are presented in Table 1. Analysis of covariance showed no significant difference between sexes for the length-weight relationship so all samples were pooled, including samples that could not be sexed (ANCOVA; n=1298, F=0.05, P>0.05, Fig. 5).
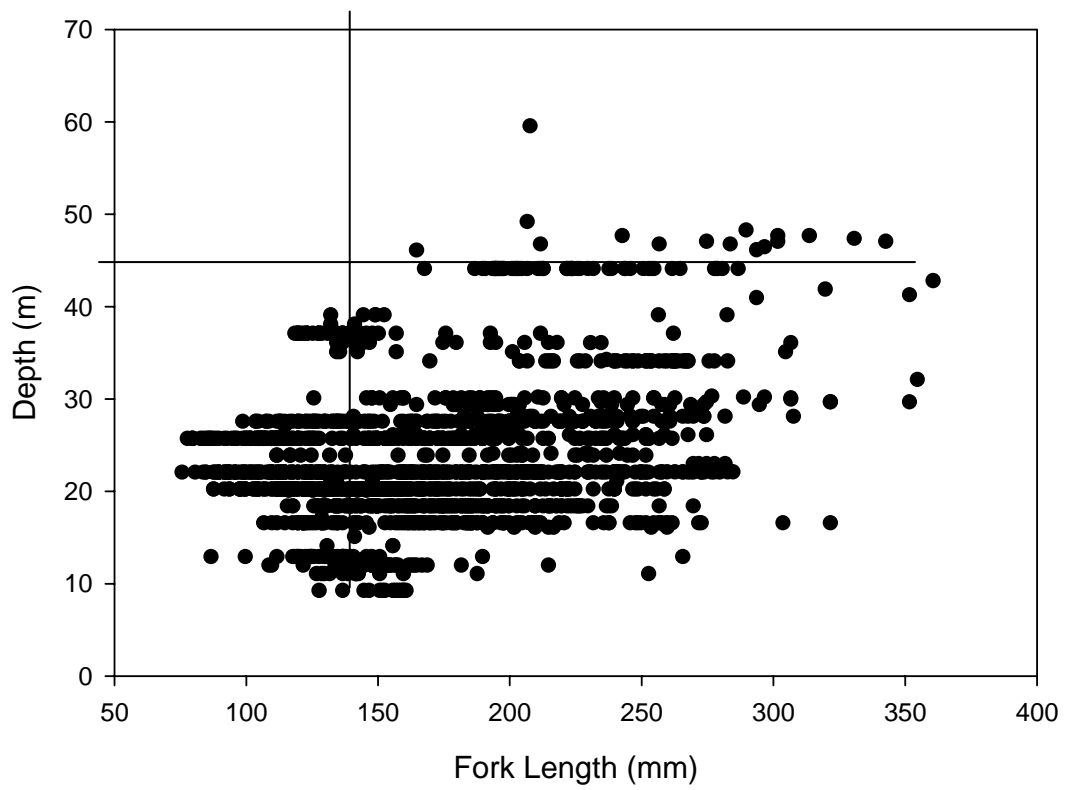
Figure 3. Relationship between depth and fork length for *Calamus proridens* collected in the northeast Gulf of Mexico.

A
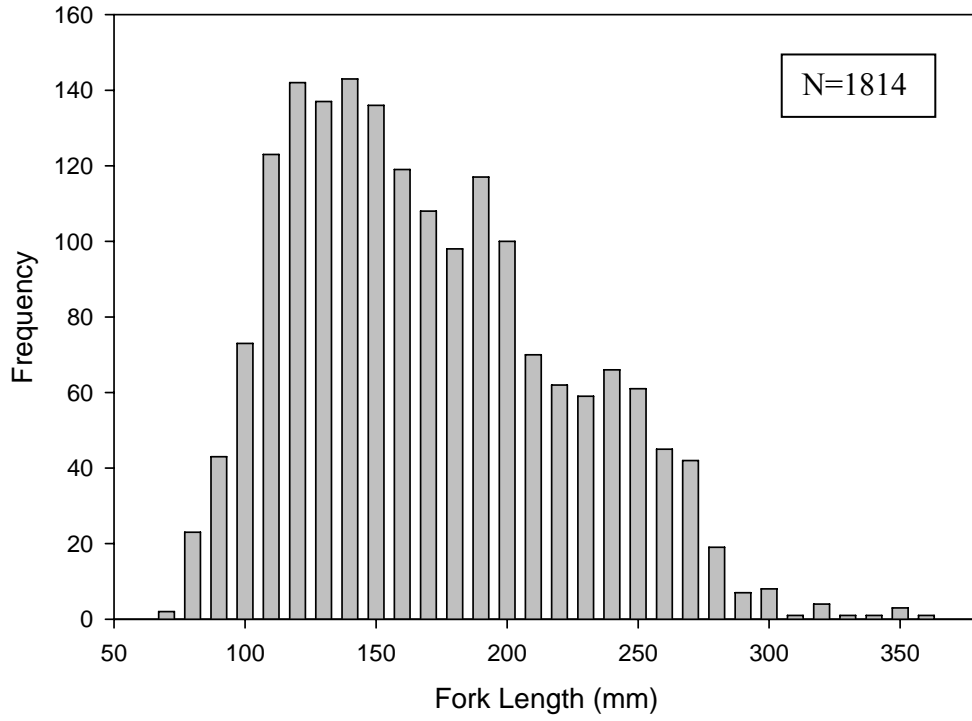
B
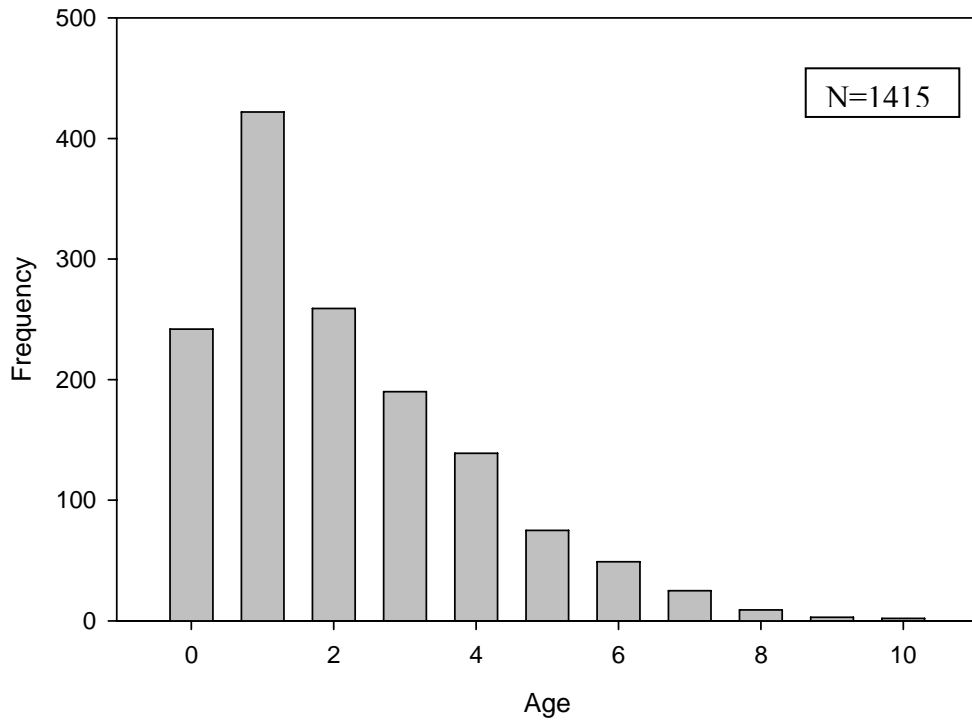
Figure 4. Length A) and age B) frequency distribution of *Calamus proridens* collected from the northeast Gulf of Mexico from 2000-2007; includes sexed and unsexed samples.

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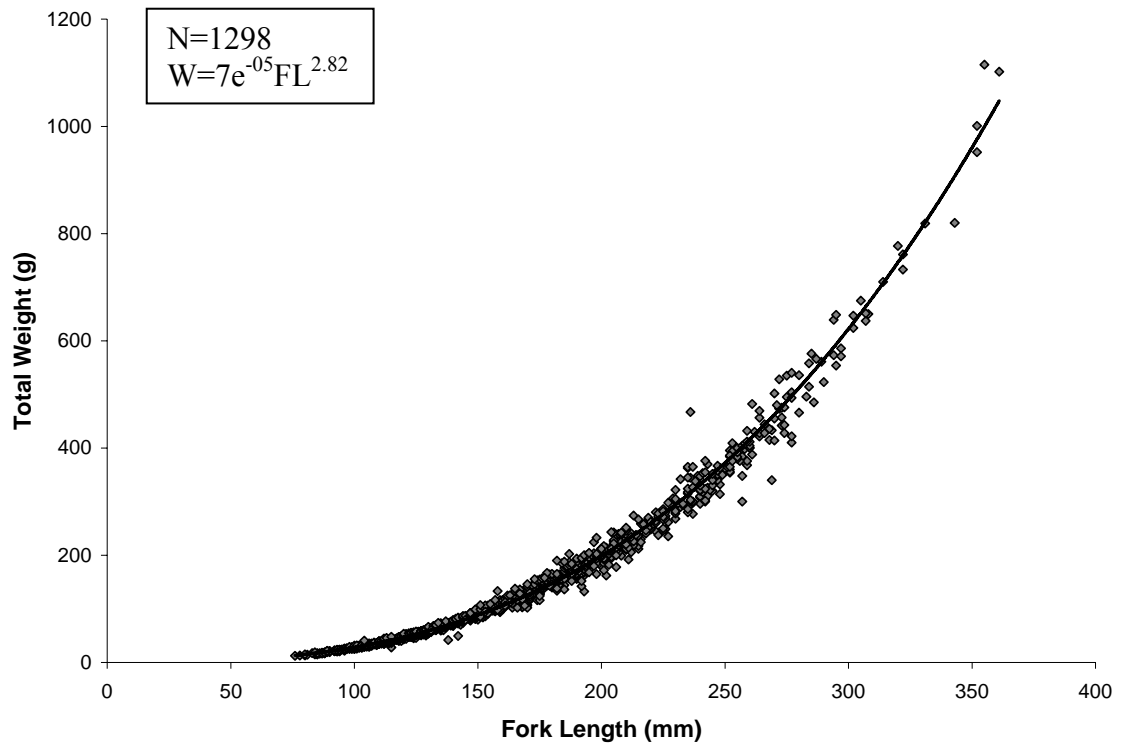
Figure 5. Length-weight relationship for *Calamus proridens* from the northeast Gulf of Mexico. There was no significant difference between sex as a result all samples were pooled for analysis, P<0.001.

Age and Growth

Otoliths were collected from 1438 specimens; 1047 were sectioned, 371 remained whole, and 22 could not accurately be aged and were not used for analysis. There was 94% agreement between the two independent reads on whole otoliths; 36 did not agree and were read a third time to produce an agreed age. Sectioned otoliths had a 95% agreement between the two independent reads, 10 samples were cut again using the right otolith and two samples did not produce an agreement on age. An agreed age was determined on all remaining samples.

Marginal increment analysis for all samples combined showed annulus deposition occurring once a year during the spring and early summer (Fig. 6). The majority of the samples were taken in April and October, which also had the largest differences in marginal increment. The mean marginal increment in April (mean=0.30, SD=0.25) was significantly smaller than the mean marginal increment for October (mean=0.69, SD=0.22, P=0.04). In April, marginal increments were either large (52%), indicating individuals were about to lay down an annulus, or were on the edge or small (38%), indicating the annulus had recently been laid down. Even though annulus deposition for individual ages could not be validated due to small sample sizes, I assumed for age and growth analysis that each opaque band represented an annual mark.

The biological intercept method for back-calculating previous length at age assumes a linear relationship between otolith radius and fish length. The relationship between otolith radius and fork length was described by the following general linear regression (Fig. 7): $FL = 211.01 * OR + 49.25$ (n = 990, $r^2 = 0.70$).

Lee's phenomenon was not observed in back-calculated lengths as there was no
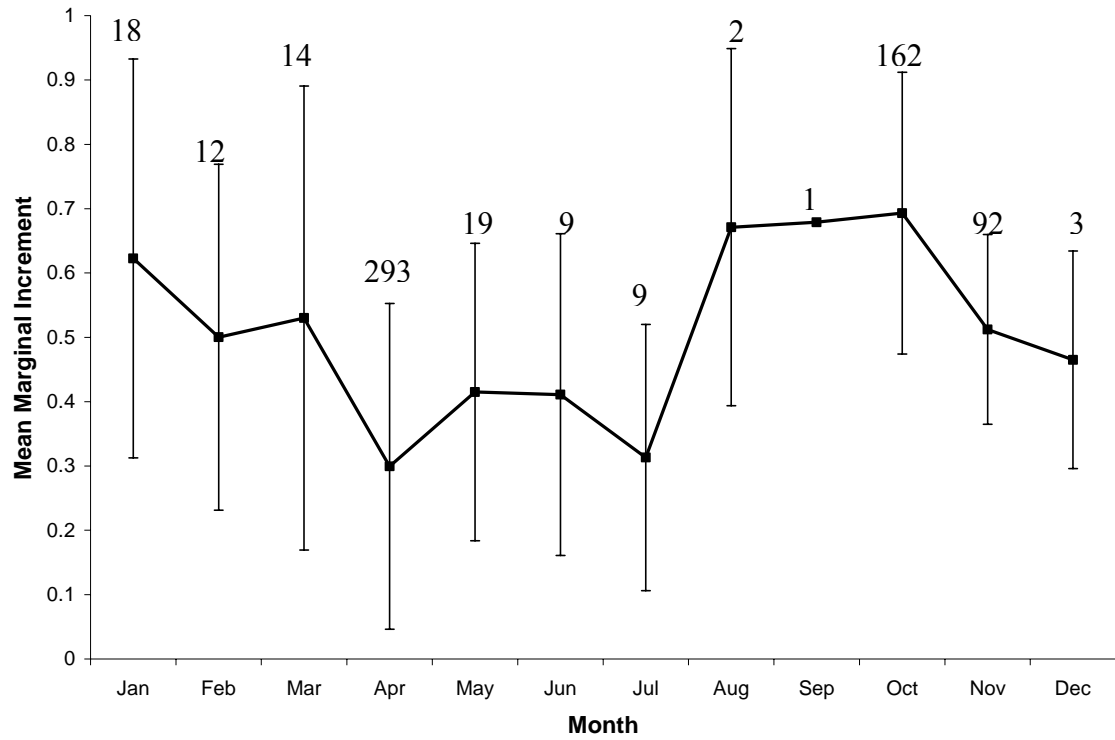
Figure 6. Mean marginal increment for *Calamus proridens* ages 2-10, n=663, error bars = standard deviation. Numbers above error bars indicate sample size.
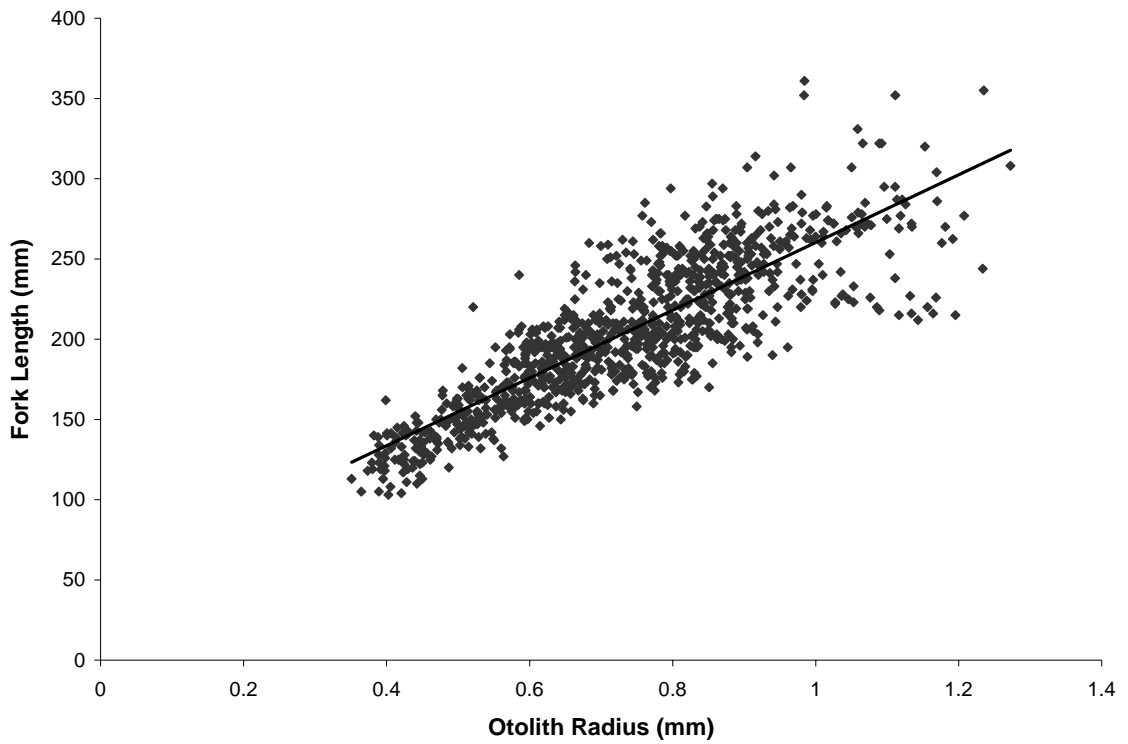
Figure 7. Relationship between otolith radius (mm) and fork length (mm). The linear regression equation is FL = 211.01x + 49.25, where FL=fork length and OR= otolith radius ($r^2 = 0.7044$, n=990).

indication that back-calculated length decreased as a function of age (linear regression, P>0.5, Fig. 8). Back-calculated lengths of *C. proridens* were 124 – 136 mm at the time of first annulus formation (Table 3) and 104 – 212 mm at age one (Table 4). The observed means for each annulus group were larger than the back-calculated means indicating that there is probably some growth after annulus formation.

Calamus proridens ranged in age from 0 to 10 and most fish (88%) were between ages 0 and 4 (Fig. 4B and Table 4). Only 14 fish (1%) were older than age seven. The largest specimen was 361 mm and was six years old. The smallest specimen collected was 76 mm and age 0. There were two 10 year olds that were 308 and 355 mm. Size increased rapidly until age two (mean size = 193 mm) where it began to level off; and over 50% percent of the total growth was completed by age two. Growth began to slow down after age three and then began to slightly increase after age six. Females were not observed after the age of six and males were observed to age 10.

The von Bertalanffy growth equation, fitted to observed length at ages (all sexes combined) was $L(t) = 306^*(1-e^{-0.254(t+1.69)})$ (Fig. 9 and Table 5). The estimated L_∞ of 306 mm appears low based on observed maximum length of 361 mm. The predicted sizes at age were similar to the observed length at age up to age 9; this could be due to the small sample size in the larger age groups (Table 6). The growth parameters estimated for the southern strata were L_∞=268.5 mm, K=0.32, t_o=-1.54, and the central strata estimated parameters were L_∞=292.9 mm, K=0.32, t_o= -1.36 (Fig. 10). The two growth curves were significantly different (P<0.01) based on the randomization analysis. It appears that
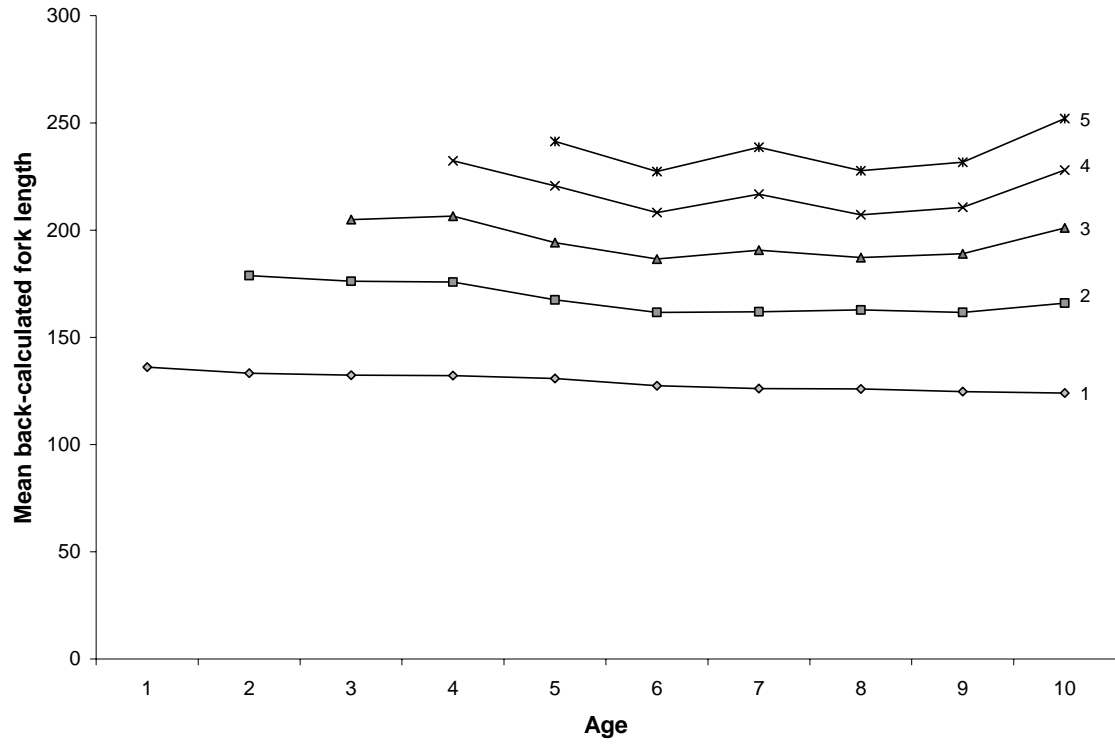
Figure 8. Mean back-calculated fork length between ages 1-5 as a function of age at capture. The lack of a significant trend (P>0.05) indicates the absence of Lee's phenomenon.

Table 3. Mean back-calculated FL at annulus formation of *Calamus proridens*, all sexes combined. Back-calculated lengths were estimated using the biological intercept method (Campana and Jones, 1992).

Annulus group	N	1	2	3	4	5	6	7	8	9	10	Observed mean ± SD
1	221	136										176 ± 22
2	165	133	179									197 ± 21
3	189	132	176	205								218 ± 26
4	130	132	176	207	232							243 ± 22
5	64	131	168	194	221	241						250 ± 24
6	43	127	162	187	208	227	244					254 ± 29
7	25	126	162	191	217	239	259	275				283 ± 31
8	12	126	163	187	207	228	245	262	277			285 ± 21
9	3	125	162	189	211	232	250	273	290	304		311 ± 18
10	1	124	166	201	228	252	274	293	309	328	347	355
Weighted means		133	174	201	223	236	249	271	281	310	347	

Table 4. Sample sizes, observed mean fork length (mm) at age, and range for *Calamus proridens*.

	Female			Male			Transitional			All		
Age	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
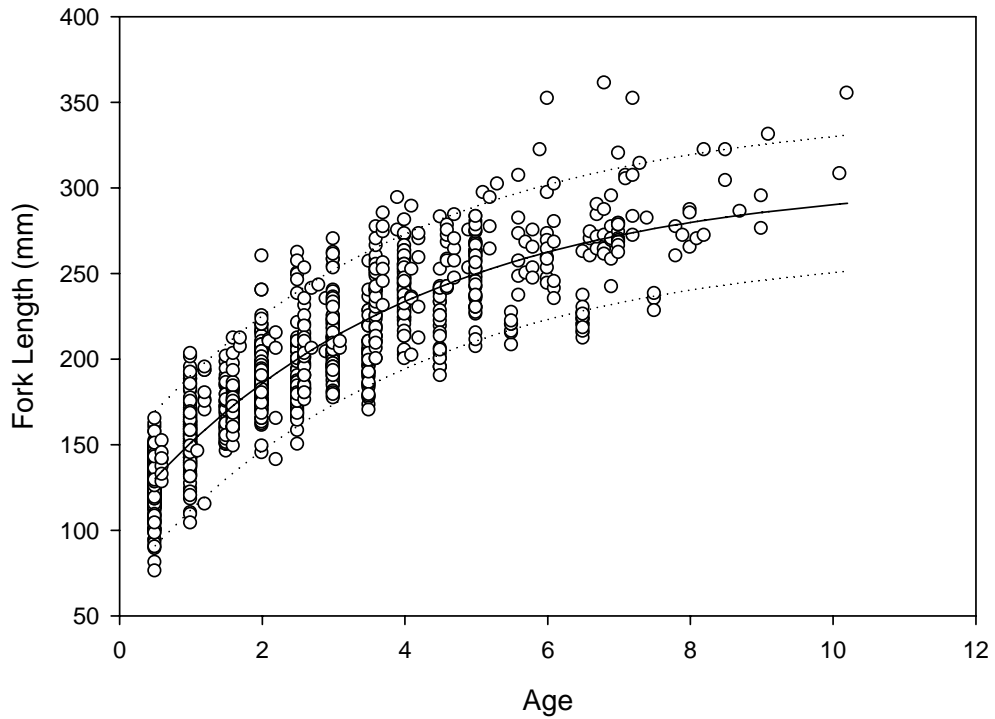
Figure 9. Von Bertalanffy growth model fitted to all observed length at age data for *Calamus proridens*. Solid line = predicted growth curve, dotted lines = upper and lower 95% confidence intervals.

Table 5. Growth parameter estimates of *Calamus proridens*, from the von Bertalanffy growth model with standard error and 95% confidence intervals. The AIC= Akaike's Information Criteria quantifying the fit of the growth model to the length at age data. Standard error for each parameter is in parentheses and the 95% CI is the lower and upper ranges.

		Parameters						
		L_∞		K		t_o		AIC
Strata	n	Estimate (±SE)	95% CI	Estimate (±SE)	95% CI	Estimate (±SE)	95% CI	
Southern	754	268.5 (5.96)	256.8 280.2	0.320 (0.026)	0.27 0.37	1.54 (0.12)	-1.78 -1.29	1892
Central	558	292.9 (6.86)	279.4 306.4	0.317 (0.025)	0.27 0.37	1.36 (0.11)	-1.56 -1.15	1395
All	1415	306.0 (5.72)	294.8 317.2	0.254 (0.015)	0.22 0.28	1.67 (0.09)	-1.89 -1.51	3688

Table 6. Sample sizes, observed mean fork length (mm) at age, and predicted length at age from the Von Bertalanffy growth model for *Calamus proridens* for all samples, and the central and southern strata.

	All			Central			Southern		
		Mean			Mean			Mean	
Age	N	(obs)	Predicted	N	(obs)	Predicted	N	(obs)	Predicted
0	242	127	130	111	129	131	131	126	129
1	422	158	157	153	162	160	259	155	154
2	259	193	192	110	200	198	136	186	188
3	190	215	218	81	219	224	100	208	211
4	139	240	236	66	241	241	58	233	226
5	75	253	252	17	255	256	43	245	236
6	49	258	267	10	260	267	17	231	247
7	25	279	274	5	276	272	8	256	252
8	9	290	281	4	295	279	1	285	255
9	3	301	286	1	295	281	1	276	259
10	2	332	291						
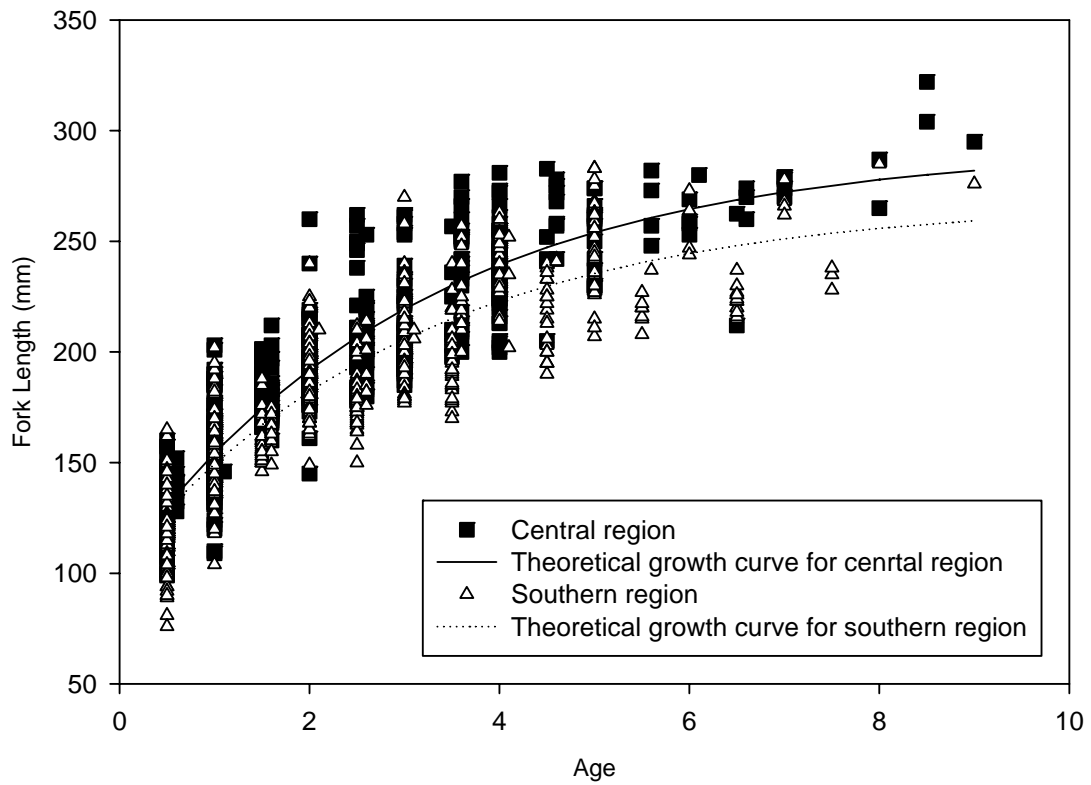
Figure 10. Von Bertalanffy growth curves fitted to observed length at age for the central and southern regions of the west coast of Florida. Parameter estimates are given in Table 5.

while the Brody's growth coefficient is the same for both strata the fish in the southern

stratum do not grow as large as the fish in the central stratum. The model predicted

lengths at age that were similar to the observed lengths at age for the central and southern

strata; again sample sizes were small for the older age group (Table 6).   While there

were not enough samples to construct a growth curve from the northern region, the oldest

fish (age 10) were collected in that region. The AIC numbers were lowest for the

southern and central data indicating a better fit to the model than when all the data were

combined (Table 5). Estimates and statistics for all growth models are presented in Table

5. An age-length key was also created for *C. proridens* based on the observed age and

length data collected (Table 7).

Table 7. Age length key for *Calamus proridens* from the northeast GOM. Length class = fork length at 20 mm intervals, N= number samples, values are proportions within each age class.

Length class (mm)	N	Age										
		0	1	2	3	4	5	6	7	8	9	10
60	1	1.00										
80	10	1.00										
100	61	0.90	0.10									
120	155	0.77	0.23									
140	256	0.21	0.77	0.02								
160	208	0.01	0.64	0.30	0.04							
180	200		0.21	0.52	0.25	0.02						
200	163		0.05	0.40	0.37	0.12	0.04	0.02				
220	114			0.10	0.30	0.33	0.15	0.10	0.03			
240	120			0.08	0.21	0.48	0.16	0.08				
260	86			0.02	0.12	0.19	0.28	0.19	0.16	0.03	0.01	
280	24				0.08	0.17	0.25	0.25	0.08	0.13	0.04	
300	9						0.22	0.11	0.44	0.11		0.11
320	5						0.20		0.20	0.40	0.20	
340	3							0.33	0.33			0.33
360	1							1.00				

Reproduction

Sex was assigned in the field to 1710 specimens; sex was unable to be determined on 104 samples. Samples were comprised of 1371 (80.2%) females, 297 (17.4%) males, and 42 (2.5%) transitionals (Table 4). Females ranged from 76 to 297 mm FL and were 0 to 6 years old (Fig. 11). The mean length for females was 156 mm, with a mean age of 1.4 years; 82% of females aged were between 0 and 2 years. Males ranged in length from 141 to 361 mm with a mean size of 244 mm. They ranged in age from 1 to 10 years old, with a mean age of 4.2 years. Over half (58%) of the males aged were between 3 and 5 years; while only a few were older than 7 years. There was a significant difference in the age and length distribution for males and females: 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). Females dominated the smaller size classes up to 190 mm, and males dominated the larger size classes (Table 8). Length at age was also significantly different for males and females for all ages except age six (ANOVA P<0.01).

The overall sex ratio (1:4.6 males to females) was significantly different from the expected 1:1 for a gonochoristic fish (X^2 = 691.5, P<0.001). Sex ratio by length class for males and females also had a significant deviation from the expectant 1:1 in all size classes except length groups 220, 230, and 290 mm (Table 8). Sex ratio was further broken down by age and again chi square analysis showed a significant deviation from 1:1 for all ages except age 4 (Table 9).

A total of 388 gonads were processed for histology and were either ovarian, ovotestes (hermaphroditic females), transitional, testicular, or hermaphroditic males.

A
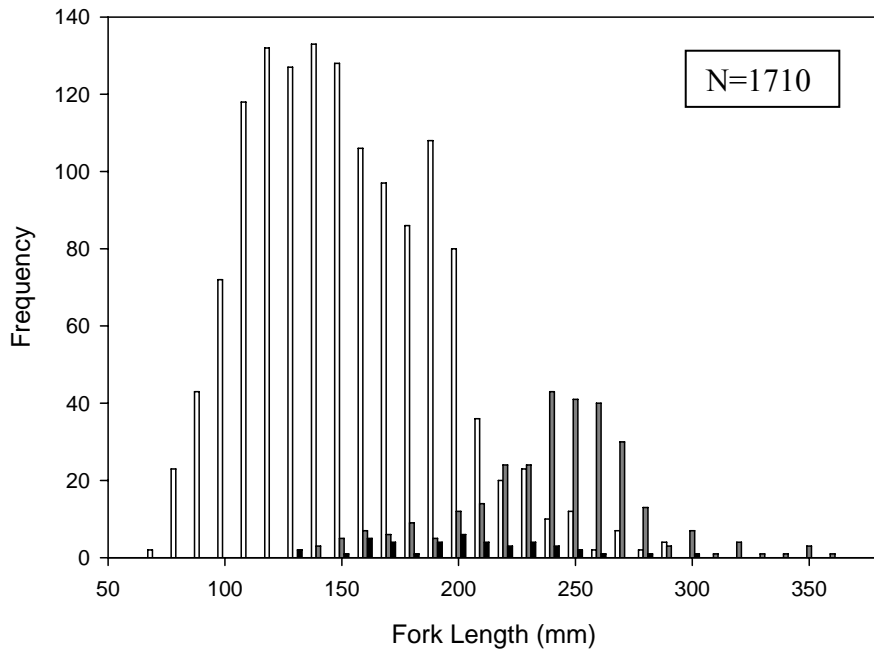
B
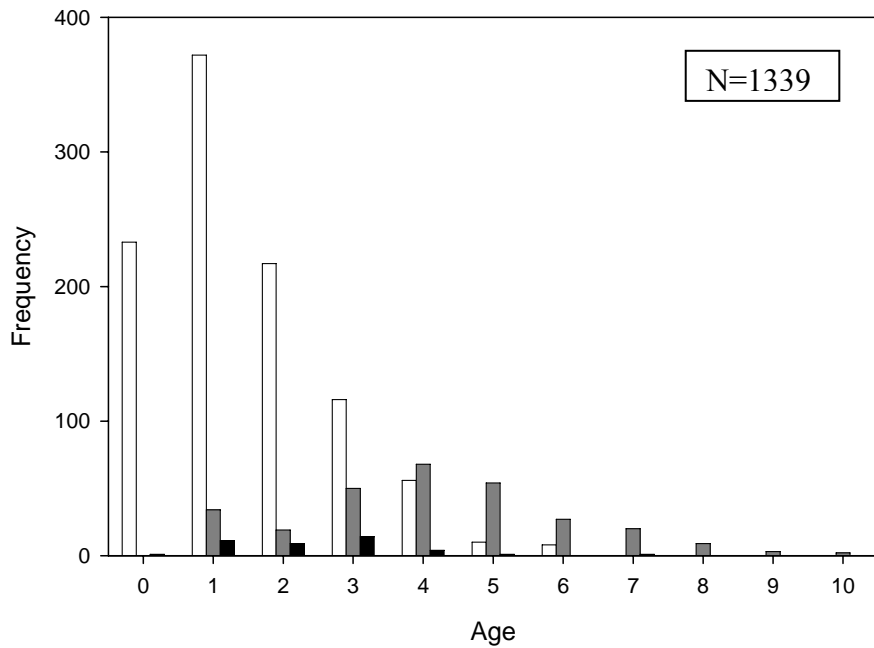
Figure 11. Length A) and age B) frequency distribution of *Calamus proridens* collected from the northeast Gulf of Mexico from 2000-2007. Females = white bars, males = dark grey bars, transitionals = black bars.

Table 8. Number and percentage of females, males, and transitionals of *C. proridens* from the northeast Gulf of Mexico grouped into 10 mm length classes with sex ratio. Chi square test was conducted to test for significant difference from a 1:1 sex ratio, * indicates P<0.01.

Length Class	Females		Males		Transitionals		Male:Female	
	N	%	N	%	N	%		
70	2	100.00						
80	23	100.00						
90	43	100.00						
100	72	100.00						
110	118	100.00						
120	132	100.00						
130	127	98.45			2	0.88		
140	133	97.79	3	1.28			1:44.33	*
150	128	95.52	5	2.18	1	0.43	1:25.60	*
160	106	89.83	7	3.37	5	2.37	1:15.14	*
170	97	90.65	6	3.04	4	1.99	1:16.17	*
180	86	89.58	9	4.85	1	0.53	1:9.56	*
190	108	92.31	5	2.39	4	1.89	1:21.60	*
200	80	81.63	12	6.68	6	3.22	1:6.67	*
210	36	66.67	14	11.60	4	3.02	1:2.57	*
220	20	42.55	24	26.80	3	2.58	1:0.83	
230	23	45.10	24	24.97	4	3.30	1:0.96	
240	10	17.86	43	58.22	3	2.27	1:0.23	*
250	12	21.82	41	53.37	2	1.54	1:0.29	*
260	2	4.65	40	83.94	1	0.76	1:0.05	*
270	7	18.92	30	53.65			1:0.23	*
280	2	12.50	13	45.61	1	1.35	1:0.15	*
290	4	57.14	3	4.68			1:1.33	
300			7	87.50	1	1.05		
310			1	100.00				
320			4	100.00				
330			1	100.00				
340			1	100.00				
350			3	100.00				
360			1	100.00				
Total	1371	80.18	297	17.37	42	2.46	1:4.62	*

Table 9. Number and percentage of females, males, and transitionals of *C. proridens* from the northeast Gulf of Mexico by age class with sex ratio. Chi square test was conducted to test for significant difference from a 1:1 sex ratio, * indicates P<0.01.

Age	Females		Males		Transitionals		Male:Female	
	N	%	N	%	N	%		
0	233	99.57		0.00	1	0.43		
1	372	89.21	34	8.15	11	2.64	1:10.94	*
2	217	88.57	19	7.76	9	3.67	1:11.42	*
3	116	64.44	50	27.78	14	7.78	1:2.32	*
4	56	43.75	68	53.13	4	3.13	1:0.82	
5	10	15.38	54	83.08	1	1.54	1:0.19	*
6	8	22.86	27	77.14		0.00	1:0.30	*
7		0.00	20	95.24	1	4.76		
8		0.00	9	100.00		0.00		
9		0.00	3	100.00		0.00		
10		0.00	2	100.00		0.00		
Total	1012	75.58	286	21.36	41	3.06	1:3.54	*

Macroscopic pictures of ovarian, transitional, and testicular are shown in Fig. 12. Ovotestes – ovarian tissue with small quantity of testicular tissue (male cyst) attached to the ovarian wall (Fig. 13) were observed in 39% of the samples 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. The majority of the ovotestes were observed in October, November, and April; however they were also observed in January, July, and December. The specimens with the testicular tissue undergoing spermatogenesis were larger and older (mean FL = 218 mm, mean age=2.3 years) than the ones only containing spermatogonia (mean FL = 165 mm, mean age=1.1 years). Ovotestes only containing spermatogonia were observed as early as age 0, while ovotestes with spermatogenesis were not observed until age 1; both were observed up to age 4.

Histological evidence confirms *Calamus proridens* is a monandric protogynous hermaphrodite. Transitionals were determined by the presence of proliferating male tissue and degenerating female tissue (Fig. 13). A total of 42 transitionals were observed, 38 of them confirmed through histology. Most specimens undergoing sex reversal ranged in size from 131-307 mm and were 1 to 5 years old (Fig. 11). One transitional was also observed at age 0 and another one at age 7. The mean size at sex reversal was 207 mm with a mean age of 2.4 years; and the majority of fish undergoing sex reversal (83%) were ages 1 to 3. The estimated age and length at which 50% of the population had transitioned from female to male was 4 years and 231 mm (Fig. 14). Transitionals were observed in January, April, July, October, and November, however, no samples were collected in September and less than 10 samples were collected in June, August, and

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Figure 12. 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.
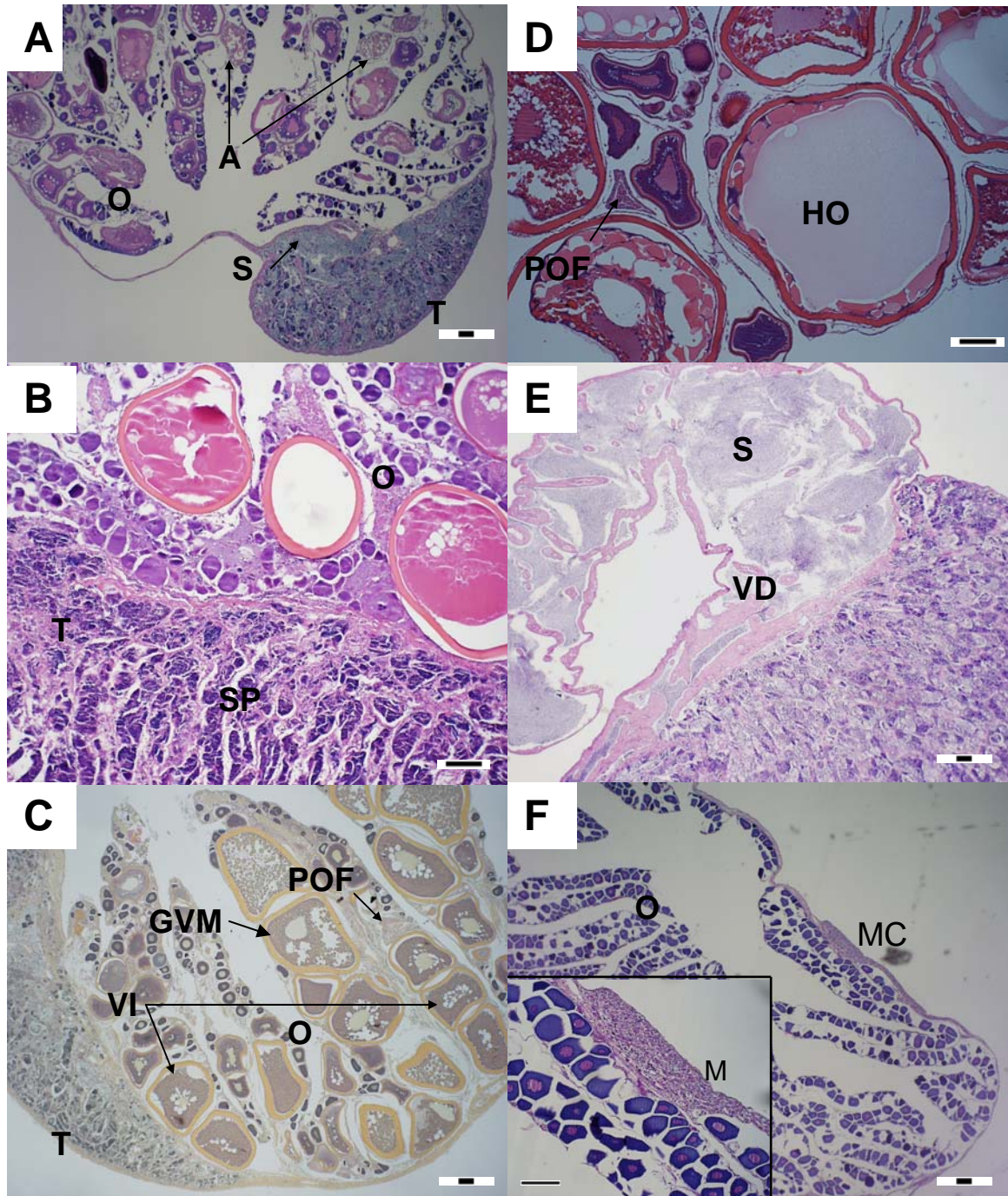
Figure 13. Histological sections of *Calamus proridens* gonads. Transitional gonads with proliferating male tissue and degenerating female tissue from A) a 131 mm FL specimen collected in April 2007, B) a 167 mm FL specimen collected in April 2003, and C) a 225 mm FL specimen collected in April 2006. D) A spawning female gonad from a 205 mm FL specimen collected in April 2003. E) A spawning male gonad from a 216 mm FL specimen collected in April 2004. F) A 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. Black scale bars are 0.1mm
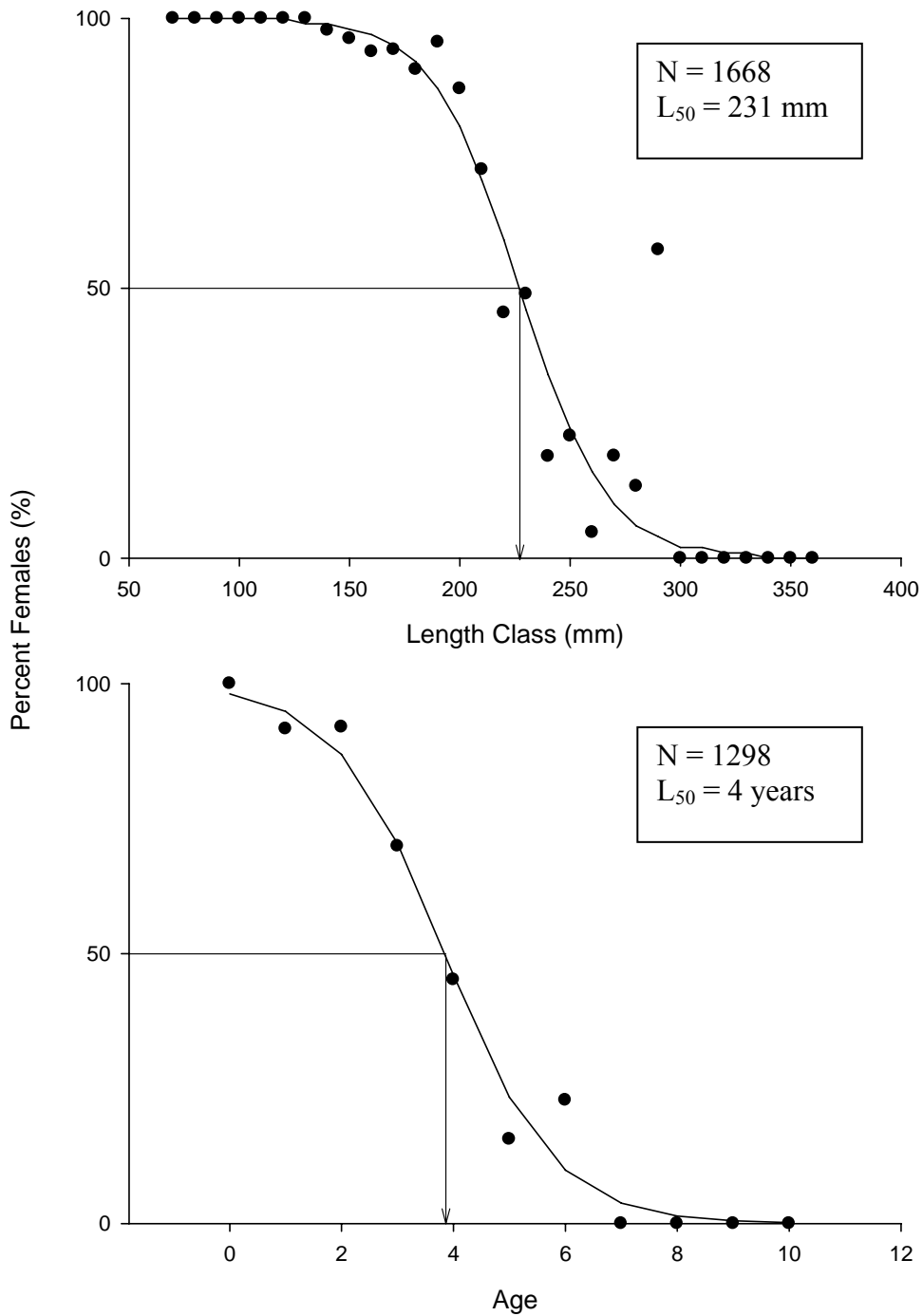
Figure 14. Percentage of female littlehead porgy, *Calamus proridens* by age and length class (10 mm size intervals) with a logistic function (continuous line) fitted to the observed data. Arrows indicate predicted length and age at which 50% percent of the females transition into males.

December. Sex reversal was most often observed (64%) during the non-spawning season in October and November when the females were usually regenerating, although transitionals were also observed 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 class. The female tissue had hydrated oocytes and post ovulatory follicle (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 was not developed.

Calamus proridens mature at a small size. Estimated size for females at 50% maturity was 132 mm (SE=2.25 mm) and maturity increased rapidly as length increased (Fig. 15). The largest immature observed was 156 mm. The logistic regression indicated that 50% of the individuals mature by the first year and all probably mature after the first year.

All reproductive classes for female gonads were observed in the histological samples. Due to difficulty with artifacts in the histology and possible postmortem degeneration of the gonad, gonads classified as spawning-capable and actively spawning were grouped together as spawning. It was also difficult to determine the difference between immature and regenerating in some gonads. In these cases, the gonads were classified as unknown when it could not be determined (n= 41). Female gonads showed signs of spawning from February through May; no samples were collected in June and by July the few samples observed were regenerating. Atretic oocytes were observed in regressed gonads during April. Spawning females ranged in size from 138-297 mm (mean = 200 mm SE=3.74). *Calamus proridens* are batch spawners and may spawn daily

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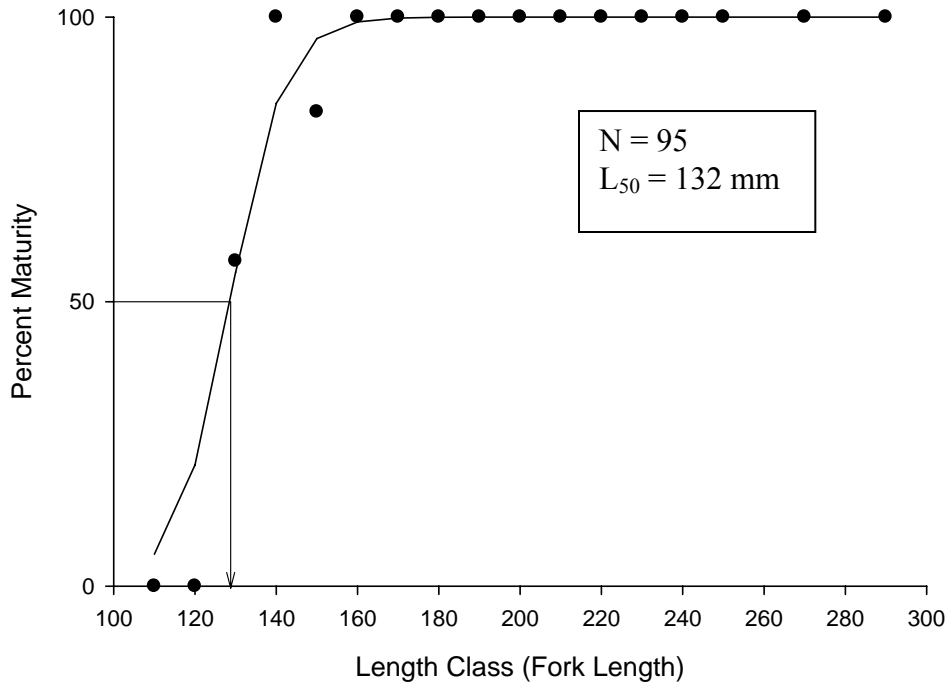
Figure 15. Percentage of mature littlehead porgy, *Calamus proridens* by length class (10 mm size intervals) with a logistic function (continuous line) fitted to the observed data. Arrows indicate predicted size at which 50% of the population was mature.

as the presence of POF's were observed with hydrated oocytes (Fig. 13). In the fall only

immature or regenerating classes were observed.

A total of 136 males were collected for histological evaluation. Hermaphroditic

males (n=38) had testes that had functional male tissue but had traces of ovarian tissue.

Timing of male reproduction was difficult to determine as the majority (89%) of the

males examined had testes with sperm. Six samples had visible sperm ducts filled with

sperm (Fig. 13) and I could clearly classify them as spawning, while nine testes only had

the presence of spermatogonia and spermatocytes and were most likely immatures.

There was no distinction or separation in length between the possible groups.

Discussion

Otoliths are a valid method for ageing *C. proridens*. Annuli on whole otoliths can be accurately counted in fish up to one year of age. However, visibility of annuli decreases in whole otoliths as fish increase in age. Scales have been used to age other *Calamus* spp. but have not had the same accuracy as otoliths (Horvath *et al.*, 1990, Waltz *et al.*, 1982). In the present study, annuli in sectioned otoliths were easily identifiable with distinct hyaline and opaque bands. The fact that only two sectioned otoliths were discarded from over 1000 samples due to disagreement emphasizes the ease and accuracy of reading sectioned otoliths for *C. proridens*. Therefore, sectioned otoliths should be the preferred method of aging *C. proridens*. Clarity of rings can decrease as age increases, a fact that should be taken into consideration when using otoliths to age older specimens of *Calamus* or other sparids.

Age validation

The use of opaque bands in otoliths to age *C. proridens* has not been previously validated. Age validation studies for *C. leucosteus,* (whitebone porgy) and *C. nodosus,* (knobbed porgy) using scales and otoliths had difficulty verifying annulus deposition (Horvath et al., 1990; Waltz et al., 1982). The marginal increment (MI) analysis in this study indicated that *C. proridens* deposited a new annulus during the spring and summer. While the marginal increment data may appear somewhat variable, the variability could be due to small sample sizes in some months. Seven months had less than 15 samples and five of those had less than 10 samples. It may be formation of the opaque band occurs

over a long period of time due to a protracted spawning period. However, a significant difference in marginal increment was observed between April (smaller MI) and October (larger MI). Annulus deposition for the red porgy, *Pagrus pagrus,* has been verified and occurs during the same time period as *C. proridens* (Hood and Johnson, 2000, Pajuelo and Lorenzo, 1996). Marginal increment analysis was able to show that annulus deposition is a yearly occurrence; however, validation for individual ages is still a good idea.

Age and growth

Results from the present study suggest that *Calamus proridens* in the GOM are moderately long-lived with an observed maximum age of 10 years and a maximum size of 361 mm. Similar maximum sizes were observed in the Campeche Bank with a maximum size of ~340 mm (type of length measurement unspecified), but ages were not determined (Dubovitsky, 1977a, Dubovitsky, 1977b). The present study is the first to determine age of *C. proridens*. There are limited age and growth studies on porgies, and of those *Calamus proridens* is most similar to the whitebone porgy, *Calamus leucosteus*, in age and size. *Calamus leucosteus* from the South Atlantic Bight had a maximum age of 12 and a maximum size of 407 mm FL (Waltz *et al.*, 1982). The red porgy, *Pagrus pagrus*, and the knobbed porgy, *Calamus nodosus,* live longer (age 18 and 17 respectively) and obtain a larger size (470 mm TL and 544 mm TL respectively) than *C. proridens* (Hood and Johnson, 2000, Horvath *et al.*, 1990)

Back-calculated estimates of length at the time of annulus deposition did not exhibit Lee's phenomenon, and were in the same range as the observed mean length at age. However, it seemed most appropriate to estimate growth curves using observed data

since the observed data had age zero fish, where back-calculated estimates did not.

The asymptotic maximum length (L_∞) of 306 mm estimated from the von Bertalanffy growth model for all data combined appeared low based on an observed maximum length of 361 mm. While separating the data based on latitude created a better fit to the model, the small number of larger and older fish could have also contributed to the low estimates of L_∞. Similar findings of low L_∞ were found with the whitebone porgy (Waltz *et al.*, 1982).

The rapid growth of *C. proridens* from the GOM in the first two years was also observed in *C. proridens* collected from the Campeche bank by Dubivinsky (1979b), even though specific growth parameters were not reported in his studies. Based on growth parameter comparisons *C. proridens* grows at a similar rate to the knobbed porgy (Hood and Johnson, 2000, Horvath *et al.*, 1990), red porgy (DeVries, 2006) and the white grunt, *Haemulon plumieri* (Murie and Parkyn, 2005). *Calamus proridens* also grew initially faster than most groupers and snappers; this could be attributed to grouper and snappers much longer life span or that most grouper and snapper studies do not have young-of-the-year data.

Calamus proridens collected in the southern strata (26º latitude – off of Charlotte Harbor) grew at a similar rate, but attained a smaller maximum size than in the central strata (27º latitude – off of Tampa Bay). Differences could be attributed to water quality, habitat, food availability, predators, competition and/or fishing pressure (Murie and Parkyn, 2005, Thurman, 2004). Local differences in size composition could be due to differences in mortality rates rather than growth rates (Murie and Parkyn, 2005). Further research on environmental parameters and additional biological studies could be collected

to further explain the differences that were observed. While there is not a commercial

fishery for *C. proridens,* they are a significant bycatch in other commercial fisheries such

as the red snapper and shrimp fishery. Even though they are not as heavily fished

recreationally as groupers, snappers, and red porgy; *C. proridens* are recreationally

fished. With increased restrictions on other reef species, fishermen will begin to fish for

species with little to no restrictions. Having data available will help obtain accurate stock

assessments and to help establish and maintain an overall ecosystem based approach to

monitoring reef species in the GOM.

An age-length key has not been previously estimated for *C. proridens*. The age

length key is another tool to use in stock assessments that can be used to estimate age for

fish caught in the northeast GOM. Based on this key fish caught between 140 – 179 mm

FL, in the northeast of the GOM, would be age one. Due to low sample sizes in the large

length classes the age length key may not be an accurate estimate for age of fish greater

than 300 mm FL. This also indicates that the largest fish are not necessarily the oldest

fish.

Reproduction

Female *C. proridens* in the northeast GOM reached maturity at a small size (132

mm) and within the first year. Research on the whitebone porgy, which in most respects

is quite similar to the littlehead porgy in life history patterns, indicated that they probably

mature at age 1 (Waltz *et al.*, 1982). They also found hydrated eggs in specimens as

small as 179 mm FL. In comparison, the red porgy matures at a greater age (ages 2 - 4)

and a larger size (226-250 mm TL) (Hood and Johnson, 2000, Kokokiris *et al.*, 1999,

Pajuelo and Lorenzo, 1996).

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The population of *C. proridens* in the northeast GOM was dominated by females as indicated by a highly skewed sex ratio towards females, a result consistent with protogyny, other sparids, and specifically other *Calamus* spp. The Campeche Bank population from Dubovitsky's (1977b) studies also showed a female skewed sex ratio, but had a smaller ratio than the GOM with a 1:2.7 in favor of females. The knobbed porgy did not show a significant bias toward females in the overall sex ratio, but this could be due to the lack of small fish in their collections. Sex ratio statistics were not reported for the whitebone porgy, but females accounted for about 80% of the smaller size classes and males accounted for 70% of the larger size classes (Waltz *et al.*, 1982).

Reproductive biology in the family Sparidae is complex. In the sparid family there are species exhibiting protandry, protogyny, and rudimentary hermaphroditism, in addition to separate sexes (Alekseev, 1982, 1983, Buxton and Garratt, 1990, Garratt, 1986). A rudimentary hermaphrodite consists of an immature intersexual gonad that later matures as a male or female with evidence of sex reversal (Buxton and Garratt, 1990). Although reproduction of many sparids has been described, mainly in South African species, there are only two studies on reproductive biology within the genus *Calamus*. The histological analysis of the present study has shown *C. proridens* to be a monandric sequential protogynous hermaphrodite, which is consistent with the criteria from Sadovy and Shapiro (1987) on hermaphroditism. The nature of sex reversal in the sparid family is of the delimited type where testicular and ovarian tissues are separated by connective tissue. In protogynous species the testicular tissue proliferates and envelops the ovarian tissue as it begins to regress; this is the opposite of other protogynous families, such as Serranidae (groupers and seabasses) (Bullock *et al.*, 1996, Cochran and Grier, 1991,

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Coleman, 1981, Fischer and Petersen, 1987, Shapiro, 1987, Thurman, 2004), Labridae (wrasse) (Shapiro and Rasotto, 1993, Warner and Swearer, 1991), and Scaridae (parrotfish) (Munoz and Warner, 2004), where one sex infiltrates within the ovarian or testicular cell wall and cannot be seen without histological evaluation. During my research, at times, I was able to see both testicular and ovarian tissue macroscopically (Fig. 11) and could define them as transitionals, however, since most transitionals were observed when the female was in the regenerating class and could not be seen macroscopically, histological evaluation was needed to fully demonstrate protogynous hermaphroditism in the genus *Calamus*.

The highly biased sex ratio toward females and the significantly different length and age distributions were further evidence for protogyny. Moreover, the fact that no males were found in the smaller size classes and that they dominated the larger sizes and older ages strongly suggested that males arise only from sex change (Fig. 10 and Table 4). The presence of an ovotestis is commonly observed in delimited gonads; however, the presence of a small testicular cyst does not mean that a female will undergo sex reversal (Kokokiris *et al.*, 1999). The presence of large females demonstrated that not all females undergo sex reversal.

The mean length of transitionals was 207 mm, which was slightly smaller than the Campeche Bank population (240 mm length measurement unspecified) (Dubovitsky, 1977b). However, a 207 mm FL converts to a 241 mm TL from the length to length conversion from Table 1 and would coincide almost exactly with Dubovitsky's findings. While the majority transitioned around the mean I did find specimens that transitioned at smaller and larger sizes (Table 4). The mean length of transitionals was always larger

than the females at the same age, which could indicate that the larger females in each age group were the first to change sex which was also observed in the protogynous common pandora, *Pagellus erythrinus* (Alekseev, 1983). The increase in growth rate after sex reversal could also be an explanation for why the mean length at age of males was larger than females.

Ovotestes are common in the sparid family and occur in a wide range of ages and sizes, indicating that sex reversal may not be limited to a specific size or age (Kokokiris *et al.*, 1999). Kokokiris et. al (1999) suggested that there were three possible pathways for sexual pattern and reproduction in the red porgy. The suggested pathways were 1) females reproduce and then change sex, 2) females change sex before reproducing as a female, or 3) the female may not undergo sex change at all and remain female (Kokokiris *et al.*, 1999). Due to the differences in size and age of observed fish undergoing sex reversal, the sexual pattern in *C. proridens* may be similar to that of the red porgy.

While many studies have tried to explain the biological reasons for hermaphroditism, one theory has not become clearly dominant. The overall goal for species survival is to maximize abundance by a high rate of reproduction coupled with a high rate of survival of offspring to reproductive age. Hermaphroditism has been one adaptation to help species reach this goal. The implications for sex reversal are particularly unclear for the sparid family. The "size advantage" model suggests that a species will change sex when it is advantageous to reproduce first as one sex and then as the other sex (Ghiselin, 1969, Munoz and Warner, 2004, Warner, 1975). From an a priori standpoint, it would seem to be most advantageous to be female when the body cavity is large and can hold more eggs, so why are the males larger in *C. proridens* and

why are females transitioning at such a small size? In other protogynous species, such as groupers and wrasses, studies have demonstrated a complex social structure that controls sex reversal (Fischer and Petersen, 1987, Warner and Swearer, 1991). Unfortunately, mating systems have only received moderate attention in the sparids, and appear to be at least as complex as their reproductive biology. One study by Buxton and Garratt (1990) described three different types of mating from three different species in the sparid family: 1) demersal spawners, 2) pair spawners, and 3) dense spawning aggregates with similarly sized individuals. Dubovitsky (1977a) suggested that *C.* proridens are sequential spawners, have different spawning grounds for different groups, and indicated that they do not form dense spawning aggregations. Mating systems within the sparids are apparently complex, knowing the mating structure for individual species would be most helpful in determining cues for sex reversal.

The sex ratio/size ratio threshold hypothesis combined with the density dependent hypothesis could explain induction of sex reversal in *C. proridens*. The sex/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 level of small to large individuals is reached for a given female (Lutnesky, 1994, Ross *et al.*, 1983, Shapiro, 1987). For example, in the size- ratio model, Ross et al. (1983), showed that in the saddleback wrasse (*Thalassoma duperrey*), 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 biased 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

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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 increase in 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, this model is similar to the sex/size-ratio model except it incorporates fish density and its effects on behaviors and simple proximity (Lutnesky, 1994). Therefore, sex change in *C. proridens* may not be as much about between-sex interactions as it is about interactions within sexes. Many variables contribute to sex reversal: environmental, biological, social/behavioral, sex allocation, density-dependent, mortality, fishing pressure, and/or population changes. More than likely it is not just one factor that influences sex change but a combination of environmental and biological factors. More detailed field and/or experimental studies on mating behaviors are needed to better understand the reasons for sex reversal in *C. proridens*.

Conclusion

Even though *Calamus* spp. provides an important commercial and recreational fishery in the Campeche Bank and in the Gulf of Mexico, the status of fishing stocks has not been determined. Life history information for many porgies is unknown or limited. The present research included life history information on age, growth, reproduction, and sex change that can be included in stock assessment models and can help manage fisheries resources in the GOM as management advances from a single-species to an ecosystem based model.

Hermaphroditic species respond differently than gonochoristic species to overfishing (Alonzo, 2003, Crabtree and Bullock, 1998). Models for estimating dioecious stocks are not appropriate for estimating stocks of sex-changing species. Size-selective fishing pressure on a hermaphroditic species could affect the overall dynamics of the population and influence sex reversal. For example, if all the males are being removed this will bias the sex ratio towards females, which may affect overall spawning success resulting, in smaller and smaller females undergoing sex reversal (Alonzo, 2003, Crabtree and Bullock, 1998, Hood and Johnson, 2000). Managing stocks of sex-changing fish will require considering the sex reversal pattern, however, it must be incorporated within the context of the mating system (Alonzo, 2003). Stock assessment models should not be based on one life history parameter, but encompass as many life history parameters as are available. Models that are limited in information must be used with caution and evaluated frequently as new information is discovered.

While this research is a start in understanding the life history characteristics of *C. proridens,* additional parameters still need to be estimated. Additional research on fecundity, mortality, behavioral, and mating characteristics are still needed to better understand the biology of the species and to improve stock assessment models.

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