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ARTICLE

A Description of Age, Growth, and Reproductive Life History Traits of Scamps from the Northern Gulf of Mexico

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Abstract

We present the first comprehensive description of the age, growth, and reproductive life history traits of scamps *Mycteroperca phenax* from the northern Gulf of Mexico. Scamps were collected from commercial and recreational vessels along the northern Gulf of Mexico in 1972–2002. Scamp age was determined using thin transverse sections of sagittal otoliths; growth increments were difficult to interpret, and age was estimated for only 85% of the 5,383 otolith sections we examined. Scamps sampled from the commercial and recreational fisheries ranged from 109 to 890 mm fork length (FL) and from 1 to 31 years of age. We fitted annual ages and observed FLs to two different von Bertalanffy growth models (standard and size-modified models). The size-modified model considered the effect of the size limit but resulted in growth parameters similar to those of the standard model (asymptotic length $L_{\infty} = 772$ mm FL; growth rate $k = 0.09$ mm/year). Histology confirmed that scamps are protogynous hermaphrodites; gonadosomatic index data indicated a prolonged spawning season (January–June, peaking in April). Females reached maturity at a median FL of 332 mm and a median age of 2 years. Scamp sizes sampled from the fisheries were similar for males (221–870 mm FL) and females (109–878 mm FL), but the larger size-classes and older age-classes were mostly composed of males. The scamp population in the northern Gulf of Mexico has never been assessed, and our data provide highly valuable model inputs.

The scamp *Mycteroperca phenax* (or *M. falcatus* from Cuba south to Brazil; Jordan and Swain 1885), a member of the family Serranidae, is distributed throughout the U.S. Atlantic and Gulf of Mexico coasts and throughout Mexico (Hoese and Moore 1977). Scamps inhabit ledges or high-relief rocky bottoms in depths of 12–73 m along the west Florida shelf (Smith 1976;

FMRI 1991). However, there is a limited amount of literature regarding the life history characteristics of the scamp throughout its spatial range. The only extensive life history research (age, growth, and reproduction) on scamps has been conducted in the South Atlantic. Scamps were collected (1972–1997) from commercial and recreational vessels and during scientific surveys in

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the coastal waters of North Carolina, South Carolina, and the east coast of Florida (Matheson et al. 1986; Harris et al. 2002). The specific life history characteristics for scamps distributed in the Gulf of Mexico are fairly unknown, as only a minor description of the scamp's reproductive behavior and seasonality is available in the literature (FMRI 1991; Coleman et al. 1996).

Scamps constitute a small component of the northern Gulf of Mexico grouper commercial and recreational landings and are primarily harvested by handline gear (e.g., bandit reel and hook and line; National Oceanic and Atmospheric Administration [NOAA], Fisheries Statistics Division, personal communication). A majority of scamps are landed commercially, with only 12% being landed by recreational fishers (NOAA Fisheries Statistics Division, personal communication), and most (76%) of those are caught in Florida waters. Scamps are not caught commercially as frequently as the other grouper species, but they normally bring higher dockside prices (FMRI 1991) and historically have been the most valuable food fish among all grouper species (Jordan and Swain 1885).

The commercial fishery for groupers began in the early 1800s, primarily targeting the red grouper *Epinephelus morio*, with a bycatch of numerous *Mycteroperca* and *Epinephelus* species (Tashiro and Coleman 1977). In 1984, the Gulf of Mexico Fishery Management Council implemented the first provisions of the Reef Fish Management Unit, which consisted of 15 lutjanids and 18 serranids, including the scamp (GMFMC 1981). With the increase in reef fish landings throughout the Gulf of Mexico in the late 1980s, the Gulf of Mexico Fishery Management Council established commercial quotas for groupers (GMFMC 1989). In 1990, the state of Florida issued a size limit (508 mm [20 in] total length [TL]) for scamps caught within state waters (<16.67 km [<9 nautical miles]; FFWCC 1990); scamps caught in federal waters (≥ 16.67 km [≥ 9 nautical miles]) were not managed under a size limit until 1999 (GMFMC 1999), when a limit of 406 mm (16 in) TL was implemented.

Given the historical amount of fishing pressure on other serranids (red grouper and gag *Mycteroperca microlepis*), particularly those managed as shallow-water groupers (GMFMC 1989), it is important to investigate the basic life history of scamps. As of the 1997 stock assessment in the South Atlantic, scamps are not undergoing overfishing and are not overfished (Manooch et al. 1998). Scamp status in the northern Gulf of Mexico is unknown and has never been assessed (NOAA 2011).

Our objective was to examine and describe life history characteristics (i.e., age, length, growth, size at age, size and age at maturity, and reproductive seasonality) of scamps based on samples collected from the northern Gulf of Mexico over a period of 30 years. We also examined histological evidence to determine whether scamps are protogynous hermaphrodites. These types of data are essential for proper modeling and management of fish stocks.

METHODS

Data Collection

Scamp otoliths and gonads were collected from 1972 to 2002 through the interception of commercial and recreational vessels that were fishing primarily along the west Florida shelf in the northern Gulf of Mexico (Figure 1). Additional scamps were collected by fishery-independent surveys. Lengths (fork length [FL] or TL; mm) and weights (whole or gutted; 0.1 kg) were recorded, and otoliths and gonads were excised in the field. Information describing catch location (latitude, longitude, depth, or National Marine Fisheries Service statistical shrimp grid) was reported with the otolith samples during routine intercepts of commercial vessels and fish houses.

Scamp Growth

Interpretation of growth increments.—Growth increments were counted from thin transverse sections of the sagittal otolith. Interpretation of whole sagittal otoliths—the method used for other serranid species (Johnson et al. 1993; Johnson and Collins 1994; Fitzhugh et al. 2003; Lombardi-Carlson et al. 2008b)—was not practical given the small otolith size in scamps (otolith weight = 0.016–0.516 g). Growth increments have been validated to be annual through marginal increment analysis of scamps collected in the South Atlantic (Matheson et al. 1986; Harris et al. 2002).

Annual increments were consistently interpreted from the ventral axis (Figure 2) using a stereo microscope (35–70 \times magnification) and a reflective fiber optic light. Otolith readers recorded the number of complete annuli along with the edge type (level of translucency = partial, complete, or opaque). Annual age assignment was completed using the date of capture, annulus count, and edge type. The timing of annulus completion for scamps was estimated to be July. If the capture date was prior to July 1 and the edge type was classified as completely translucent, then 1 year was added to the reader count to calculate the annual age; otherwise, the number of complete annuli equaled the annual age.

Age agreement between readers.—Two readers interpreted scamp otoliths. The primary reader examined all otoliths, and the secondary reader completed a 20% overlap of the primary reader's otolith reads. Indices of reader agreement (average percent error [APE], coefficient of variation, and percentage of readings in agreement within ± 1 –2 bands) were calculated by following the procedures of Campana (2001).

Age and growth.—Differences in age and length data between data collection sources (commercial and recreational) were investigated. Differences in mean scamp size and age by data source and gender were examined using Student's *t*-test with unequal variances (*t*-test function in R software; R Development Core Team 2011). In addition, observed mean size-at-age data between data sources and between genders were visually inspected by plotting mean sizes (± 2 SE) at age.

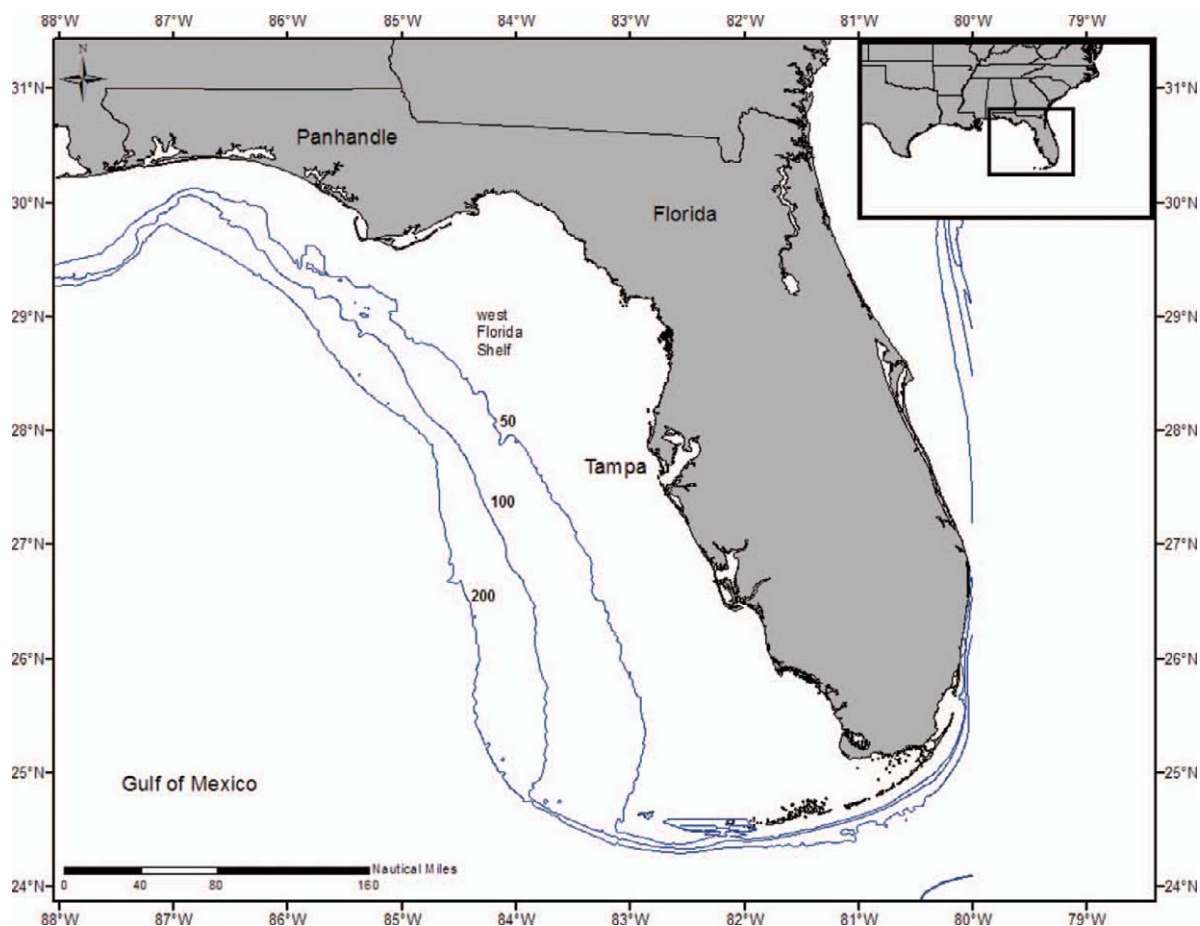


FIGURE 1. The west Florida shelf in the northern Gulf of Mexico, the primary harvest area where scamps were intercepted from commercial and recreational vessels. Depth contours are in meters.

Calculating growth from data collected from fishery-dependent sources can be troublesome, especially since most fishery-dependent data are collected under a minimum size limit (Haddon 2001). Therefore, to better predict growth, we used two different models of the von Bertalanffy growth function to fit annual ages and observed FLs. The first growth model was a standard von Bertalanffy growth function without any parameters constrained. The second growth model was a size-modified von Bertalanffy growth function (Diaz et al. 2004; Lombardi-Carlson et al. 2008b). Both models were fitted by minimizing the least squares and using the Solver routine in Microsoft Excel.

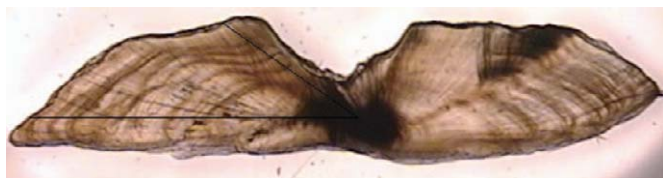


FIGURE 2. Sectioned otolith of a 500-mm (fork length) female scamp. Age was determined by interpreting opaque increments along the ventral axis (solid line) and sulcus (dotted line) using reflected light at 35 \times magnification.

The size-modified growth model was additionally fitted by taking into consideration the nonrandom sampling due to minimum size restrictions (Diaz et al. 2004). This model used a maximum negative log-likelihood estimation procedure that assumes constant SDs of size at age, sigma as the global variance for SD, and a left-normal truncated error distribution as the minimum size limit (recreational limit beginning in 1990 = 466 mm FL; commercial limit beginning in 1999 = 377 mm FL; McGarvey and Fowler 2002).

Reproduction

Gonad processing.—Scamp gonads were weighed to the nearest 0.1 g and fixed in 10% neutral buffered formalin for a minimum of 2 weeks. Preserved gonads were randomly subsampled along the anterior–posterior axes of the gonad, and a small subsample (1 cm³) was removed and placed in a cassette for histological processing. Histological processing of scamp gonads collected during 1972–1980 occurred at the Florida Fish and Wildlife Conservation Commission; all other samples were prepared by the School of Veterinary Medicine’s Histopathology Laboratory at Louisiana State University, Baton Rouge. Tissues

TABLE 1. Description of female and male scamp maturation classes based on histological preparation of gonad tissue.

Maturation class	Maturation description
Immature, inactive	Female: primary growth oocytes only; no evidence of prior spawning. Male: includes males with spermatogonia and no evidence of spermatogenesis; difficult to distinguish from regressed, except that immature males do not have residual spermatozoa.
Inactive, uncertain	Female: only primary growth oocytes are present; not capable of spawning in the distant future, and any evidence of prior spawning is unclear. Male: this phase has not been observed for males.
Developing virgin	Female: cortical alveolar oocytes predominate, and there are no indicators of prior maturity. Male: spermatogenesis begins, spermatocytes are present, and there are no indicators of prior maturity.
Developing	Female: cortical alveolar oocytes are present; indicators of prior spawning confirm maturity. Male: spermatogenesis and the formation of spermatocytes begin; few or no spermatozoa are present.
Active, mature	Female: vitellogenic oocytes are present, and fish should spawn within days or weeks. Male: this phase is not used for males since it is essentially the same as developing except that discontinuous germinal epithelium is present at either the periphery or ducts.
Spawning, hydrated (females); spawning capable (males)	Female: early or late hydrated oocytes; spawning now or within hours; also includes gonads with any stage of postovulatory follicles present. Male: fish is reproductively active and capable of spawning; all stages of spermatogenesis may be present; spermatozoa are evident and filling the lobules and sperm ducts.
Postovulatory, spent	Female: all oocytes stages may be present; the majority of oocytes (>50%) are experiencing atresia. Male: spermatogenesis is ceasing, some residual spermatozoa are present, and proliferation of spermatogonia is common.
Regressed, inactive, mature	Female: primary growth oocytes only; evidence of sexual maturity and recent spawning. Male: spermatogonia predominate, there is no active spermatogenesis, and some residual spermatozoa may be present.
Regressed, skipped, mature	Female: sexually mature but will not spawn in the current season; development ended prematurely. Male: this phase has not been observed for males.

were embedded in paraffin, sectioned to a thickness of 4–6 μm , mounted on glass slides, and stained with hematoxylin-1 and eosin-Y following standard histological procedures.

Assigning maturation stages.—Histological slides were viewed using a compound microscope at 40–400 \times magnification to determine sex and reproductive class. Gonads were staged using oocyte developmental characteristics (Wallace and Selman 1981; Hunter and Macewicz 1985; Tyler and Sumpter 1996) and were assigned to histological classes (Table 1) based on leading gamete stage, indicators of prior spawning, and short-term atresia (Lombardi-Carlson et al. 2008a). Specimens with developing, active, spawning, or resting gonads were considered sexually mature. Females that possessed only cortical alveolar oocytes were considered mature only if indicators of prior spawning were present (Rideout et al. 2000; Rhodes and Sadovy 2002). Evidence of prior spawning is described by the presence of old hydrated oocytes, the stage of atresia, the condition of the muscle bundles, the presence of connective tissue, the appearance of lamellae in the gonad tissue, and the number of macrophages (brown bodies; Lombardi-Carlson et al. 2008a). Gonads were considered to be undergoing sexual transition if at least three male gamete stages (primary spermatocyte to spermatozoa) were observed proliferating throughout the gonad and if

oocytes were remnant and possibly undergoing atresia (Sadovy and Shapiro 1987).

Histology agreement between readers.—Two readers interpreted histological slides. The primary reader examined all of the histological slides, and the secondary reader completed a 20% overlap of the primary reader's slide readings. Cohen's kappa (K ; Cohen 1960) was used to examine the agreement between the two readers (Gerritsen and McGrath 2006). The K -statistic ranges from -1 to 1 , where -1 indicates complete disagreement and 1 indicates complete agreement.

Estimates of maturity and sexual transition.—Size and age at maturity and at transition were determined using a logistic regression model:

$$Y_i = \{\exp[a + (b \cdot x_i)]/[1 + \exp(a + (b \cdot x_i))]\},$$

where Y_i = the proportion mature at length or age x_i , a = the intercept, and b = the steepness of the logistic regression. The model provides an estimate of size or age at which 50% of the population is mature (or has transitioned). Parameters a and b were estimated using a general linear model with the binomial family and logistic option in R software (R Development Core Team 2011).

TABLE 2. Number of otolith-aged scamps sampled from the northern Gulf of Mexico.

Year	Data source				Total
	Commercial fishery	Recreational fishery	Fishery-independent samples	Unknown	
1970–1979	183	11	0	77	271
1980–1989	198	10	0	17	325
1990–1999	1,127	617	56	6	1,806
2000–2002	2,787	99	94	1	2,981
Total	4,295	837	160	101	5,383

Spawning season.—The gonadosomatic index (GSI) was calculated for males and females as $GSI = [GW/(TW - GW)] \times 100$, where GW = gonad weight (g) and TW = total fish weight (g). Monthly mean GSI values were calculated to estimate seasonal reproductive patterns by sex.

RESULTS

Data Collection

Scamps were intercepted primarily from commercial vessels (80%) that used an assortment of fishing gear (handline, bandit rigs, longline, traps, etc.) and from recreational fishers (16%) that used handlines; a few scamps (160 fish) were collected by fishery-independent surveys (1990–2002; Table 2). The majority (89%) of the scamps aged were collected in 1990–2002 (Table 2), whereas most of the gonads were collected in the 1970s (35%) and 1990s (39%; Table 3).

Interpretation of Otoliths and Age Agreement between Readers

In total, 6,333 otoliths were sectioned. Interpretations of growth increments were difficult, and not all otolith sections were readable (ages were estimated for 85% of the otoliths). Two readers completed double reads of 1,426 otoliths (23% overlap). Based on acceptable values of APE (5%) as reported in the literature, scamp APE was moderate (APE = 7.73%; Campana 2001). Percent agreement values were also low (30%), but percent agreement between readers increased tremendously for estimates within ± 1 bands (68%) and ± 2 bands (88%). An age bias plot revealed that the secondary reader underestimated

scamp ages starting at age 10 (Figure 3). The primary reader's ages were used for further analysis.

Age and Growth Analysis

Scamps caught by the commercial fishery had normally distributed length and age distributions, but recreational catches had slightly skewed length and age distributions (Figure 4a, b). On average, scamps caught by the recreational fishery were significantly smaller in length (Student's t -test: $t = 20.31$, $df = 1$, $P < 0.001$) and were significantly younger ($t = 25.46$, $df = 1$, $P < 0.001$) than fish caught by the commercial fishing industry. However, there was not a consistent pattern of recreationally caught fish being smaller at all ages (Figure 4c).

Scamp annual ages and observed FLs were fitted to two growth models. The standard growth model predicted scamps to have an asymptotic length (L_{∞}) of 772 mm, a growth rate (k) of 0.09 mm/year, and a theoretical age at zero length (t_0) of -4.40 years. The growth parameters for the size-modified growth model ($L_{\infty} = 765$ mm; $k = 0.09$ mm/year; $t_0 = -3.86$ years; $\sigma = 62.14$) were similar to those of the standard growth model. The size-modified growth model had the better fit of the two models (sum of squares, standard model = 1.92×10^7 ; sum of squares, size-modified model = 2.69×10^4). The standard and size-modified growth models predicted sizes at age that were similar to observed sizes at age (Figure 5).

Interpretation of Histological Slides and Histology Agreement between Readers

In total, 2,481 histological slides were available for analysis. Histological sex and class were determined for nearly all

TABLE 3. Number of gonads examined from scamps sampled in the northern Gulf of Mexico.

Year	Data source				Total
	Commercial fishery	Recreational fishery	Fishery-independent samples	Unknown	
1970–1979	563	47	7	246	863
1980–1989	143	24	0	30	197
1990–1999	492	420	51	2	965
2000–2002	305	77	73	1	456
Total	1,503	568	131	279	2,481

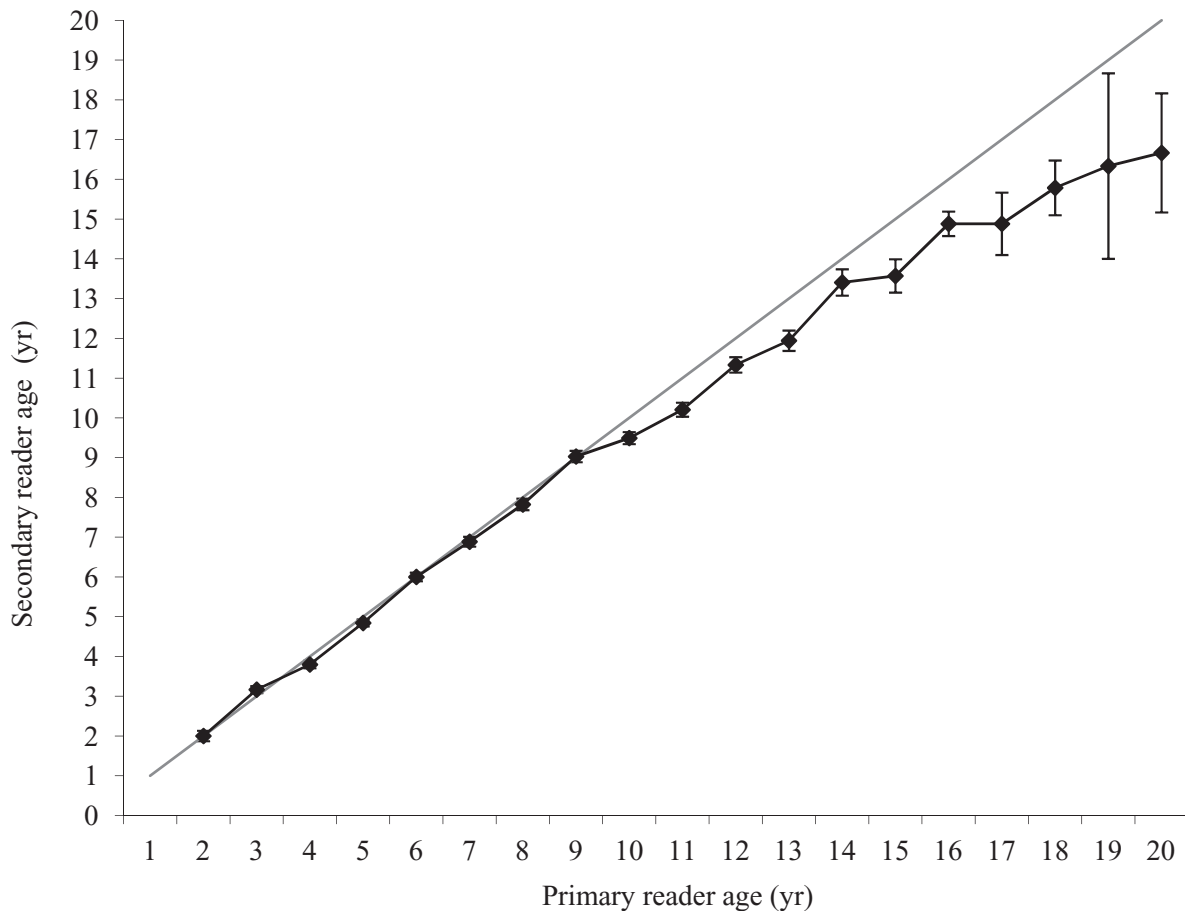


FIGURE 3. Age bias plot of 1,426 scamp otoliths sampled from the northern Gulf of Mexico and aged by two readers; the secondary reader's age estimates (mean \pm SE) are plotted against the primary reader's age estimates (yr = years). The gray line is the reference line of 1:1 agreement. Note that the secondary reader consistently underestimated age (relative to ages assigned by the primary reader) starting at age 10.

slides (92%). Two readers completed double reads of 600 histological slides for a 20% overlap. Results from Cohen's K analysis indicated that reader agreement was substantially good ($K = 0.72$). Readers had strong agreement (73%) for active and postspawning histological classes and had over 80% agreement for fish classified as regressed and spawning. The majority of disagreements occurred in the designation of immature, regressed, skipped, and unknown histological classes. Due to the difficulty in assigning fish to these histological classes, both readers reviewed these histological slides together to determine the final histological classification to be used for further analysis.

Analysis of Reproductive Traits

Females ranged from 109 to 878 mm FL, whereas males ranged from 221 to 870 mm. Males were more prevalent in the larger size-classes and older age-classes (Figure 6a, b). On average, females had significantly smaller lengths (Student's t -test: $t = -30.11$, $df = 1$, $P < 0.001$) and were significantly younger ($t = -20.69$, $df = 1$, $P < 0.001$; Figure 6a, b) than males. Males

were larger at age, with no overlap of error bars for most age-classes (Figure 6c). A small percentage (10%) of scamps were in the transitional stage, and these fish were caught primarily (72%) during the spawning season. Transitional scamps ranged from 398 to 630 mm FL and from 4 to 14 years of age.

Estimates of Maturity and Sexual Transition

Although a large size range (109–878 mm FL) of scamps was collected, only a small proportion consisted of immature fish. It is difficult to determine the difference between an immature male and a resting male during the nonspawning season. Therefore, our classification of maturity in males is based on our subjective interpretation of the spermatogenesis stages. No immature males were identified, but two inactive mature males were collected (595 mm FL, age 11, collected in December 1991; 598 mm FL, age 5, collected in October 1991). Immature females ($n = 102$) were sampled throughout the time period and had an average FL of 345 mm and an average age of 3 years. The smallest mature female was 275 mm FL (age 2) and was captured in May 1999. Females reached maturity at a median

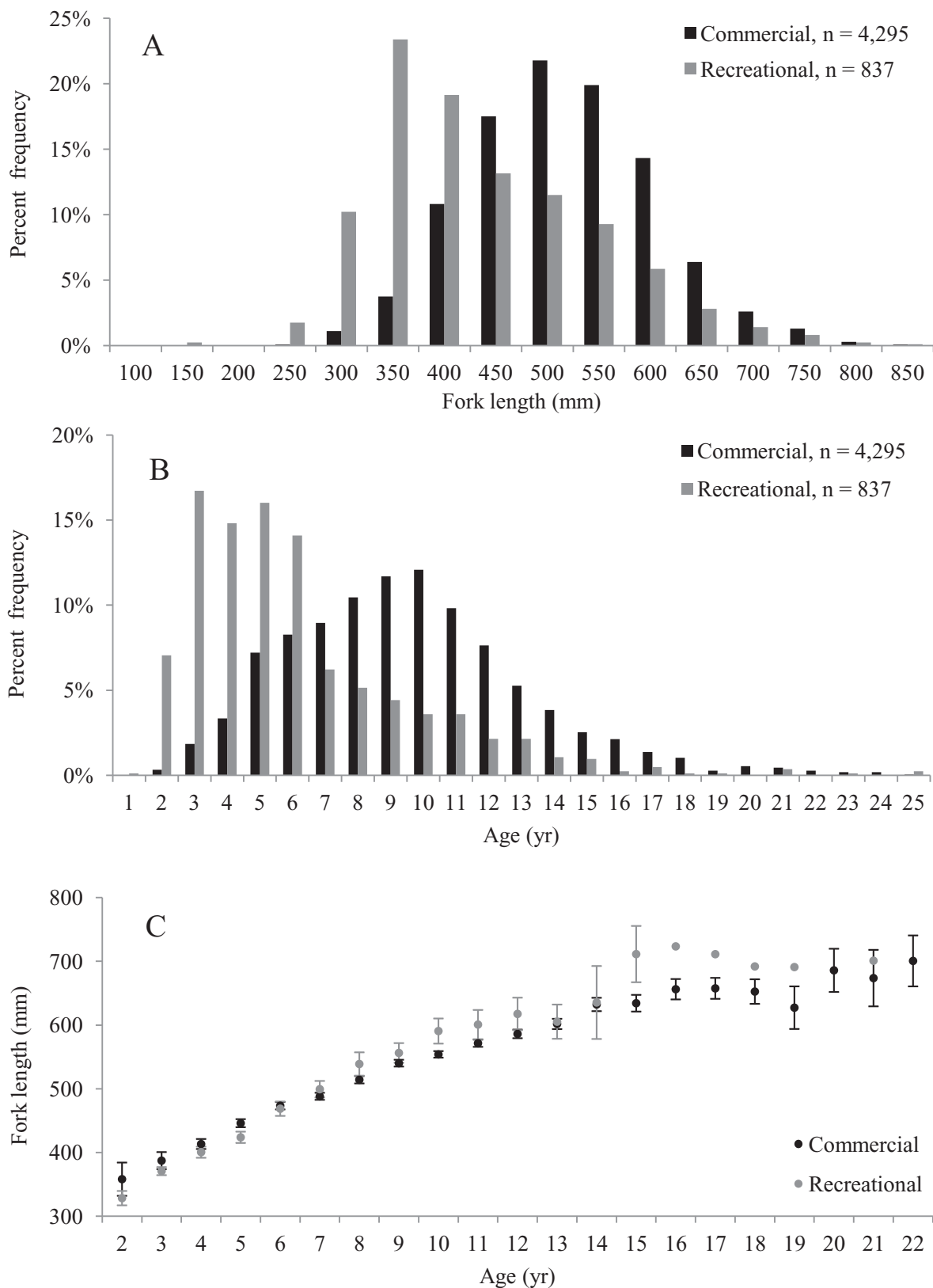


FIGURE 4. (A) Fork length and (B) age distributions (yr = years) for scamps sampled from commercial and recreational fisheries in the northern Gulf of Mexico; and (C) mean (± 2 SE) fork length at age of scamps in commercial and recreational samples.

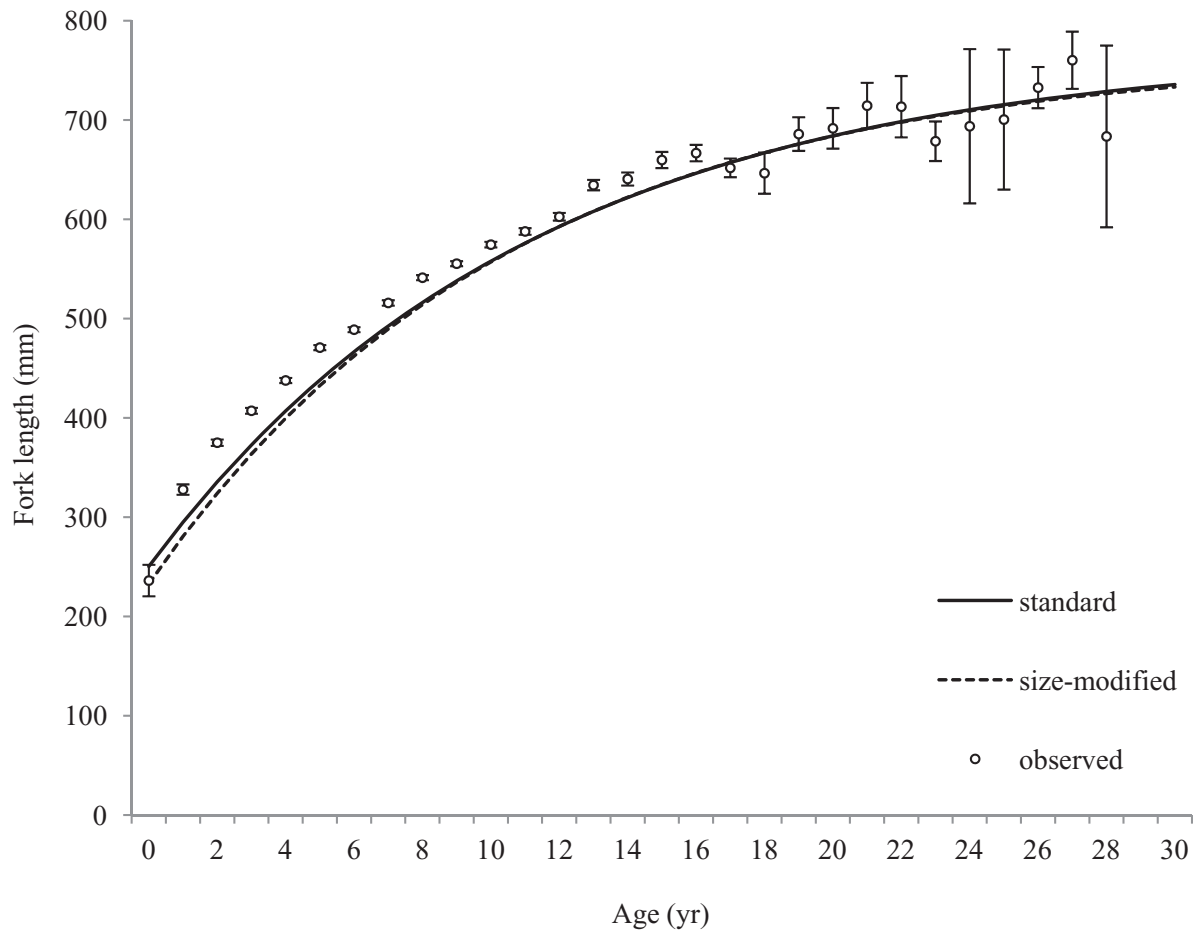


FIGURE 5. Comparison of mean (\pm SE) observed size at age (yr = years) and the sizes predicted by standard and size-modified von Bertalanffy growth models for scamps in the northern Gulf of Mexico.

FL of 332 mm and a median age of 2 years (Figure 7; Table 4). Scamps transitioned to males at a median FL of 566 mm and a median age of 11 years (Figure 8; Table 4).

Spawning Season

Based on GSI results, we concluded that scamps have a prolonged spawning season. Scamps spawn from January through June, with peak spawning in April (Figure 9). Evidence

TABLE 4. Estimates of the median size (fork length [FL]; mm) and age (years) at maturity and at transition for scamps sampled from the northern Gulf of Mexico. Parameters a and b were calculated using a general linear model with the binomial family and logistic option in R software (R Development Core Team 2011).

Variable	a	b	Estimate
FL at maturity	-11.287	0.034	332
Age at maturity	-1.866	0.927	2
FL at transition	-9.638	0.017	566
Age at transition	-3.585	0.335	11

suggested that scamps are indeterminate spawners since most female gonads contained different stages of oocyte development (i.e., cortical alveolar and late hydrated) during the spawning season.

DISCUSSION

Our results provide the first comprehensive description of age, growth, and reproductive life history traits for scamps from the northern Gulf of Mexico. Scamps collected from the commercial and recreational fisheries reached FLs of up to 890 mm and attained ages of up to 31 years. We predicted scamps to have a moderate growth rate (0.09 mm/year) and an L_{∞} (772 mm FL) that was well within the observed lengths. Females were capable of spawning at 332 mm FL and at age 2. Scamps have a prolonged spawning season (January–June), with peak spawning occurring in April; this seasonality is similar to that previously documented in the northern Gulf of Mexico (Coleman et al. 1996; Table 5). Through detailed histological photomicrographs (Figure 10) depicting the simultaneous occurrence of

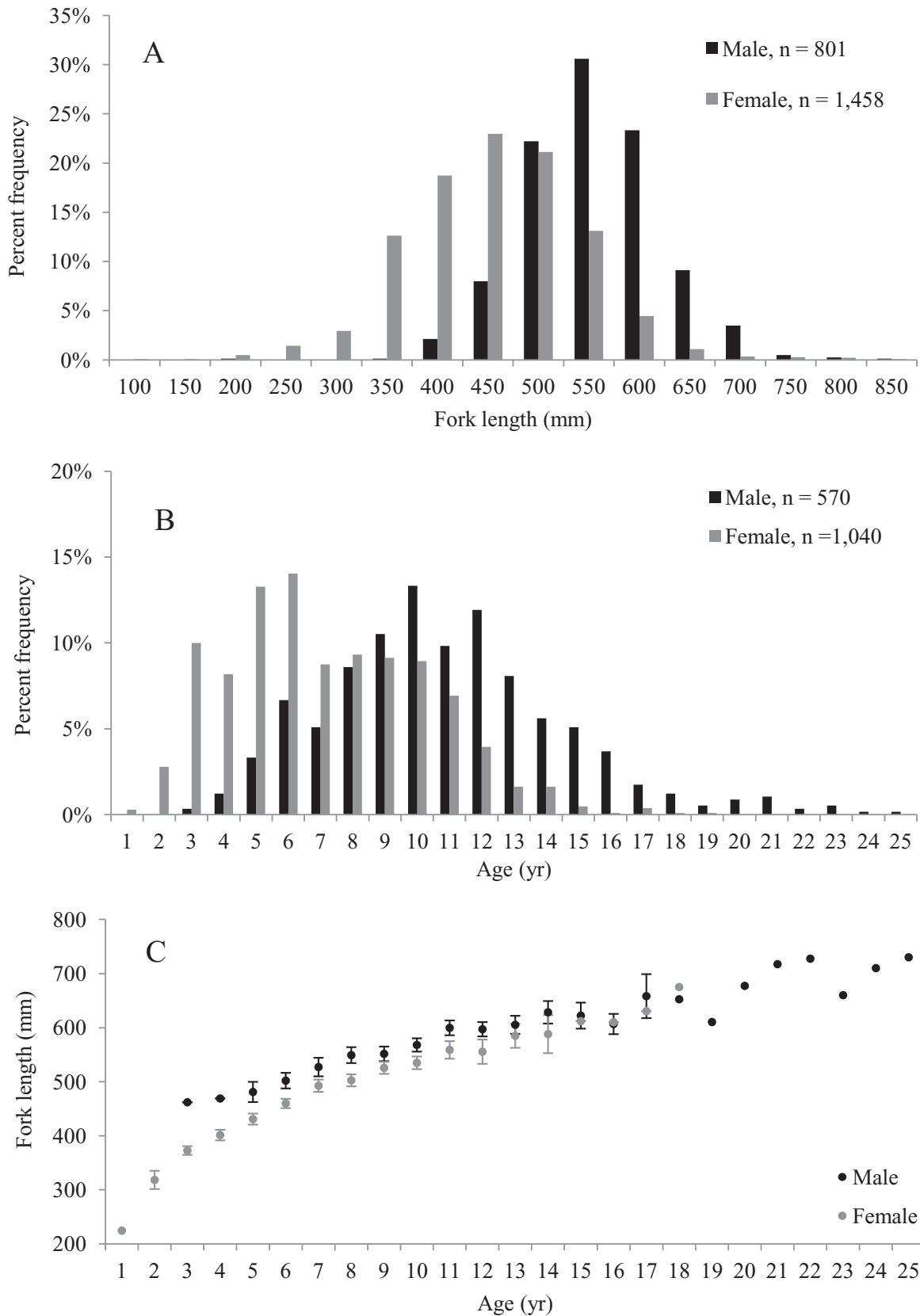


FIGURE 6. (A) Fork length and (B) age distributions (yr = years) for male and female scamps sampled from the northern Gulf of Mexico; and (C) mean (± 2 SE) fork length at age for males and females.

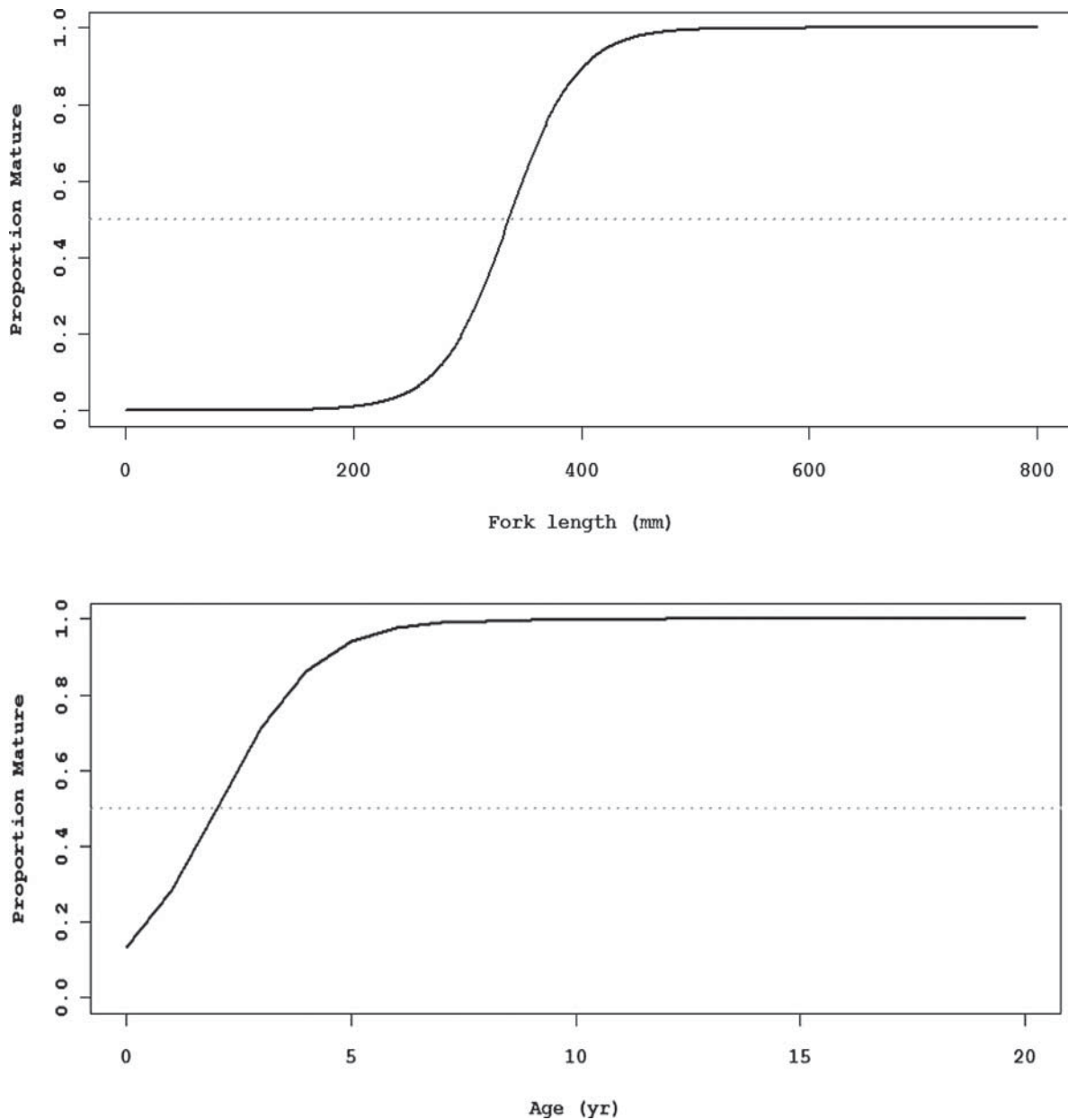


FIGURE 7. Fork length at maturity (upper panel) and age at maturity (lower panel; yr = years) of female scamps sampled from the northern Gulf of Mexico. In both panels, the solid black line represents the logistic regression and the dashed gray line represents 50% maturity (i.e., proportion mature = 0.50).

mature testicular and ovarian tissues, we also provide strong evidence that scamps from the northern Gulf of Mexico are protogynous hermaphrodites. These data are essential to properly assess this stock in the future.

Scamps constitute a small component (<3%; annual average commercial landings = 154 metric tons; Figure 11) of the Gulf of Mexico shallow-water grouper commercial and recreational landings, but an understanding of how the scamp population from the west Florida shelf has been altered by fishing is still of importance. Since 1990, scamps in state waters have been managed under a minimum size limit of 508 mm (20 in) TL (FFWCC

1990) within the annual commercial landings for shallow-water groupers (GMFMC 1989). In federal waters, the size limit is 406 mm (16 in) TL (implemented in 1999; GMFMC 1999). It is important to note that even with 30 years of fishing pressure on scamps, there have been minimal shifts in their life history parameters (mean size at age, growth rate, size at maturity, etc.; Lombardi-Carlson et al. 2011). Of most importance is that size at maturity has remained below the minimum size limit. It is possible that this minimum size limit has provided a refuge for scamps to successfully reproduce and contribute to the population before being harvested (Myers and Mertz 1998).

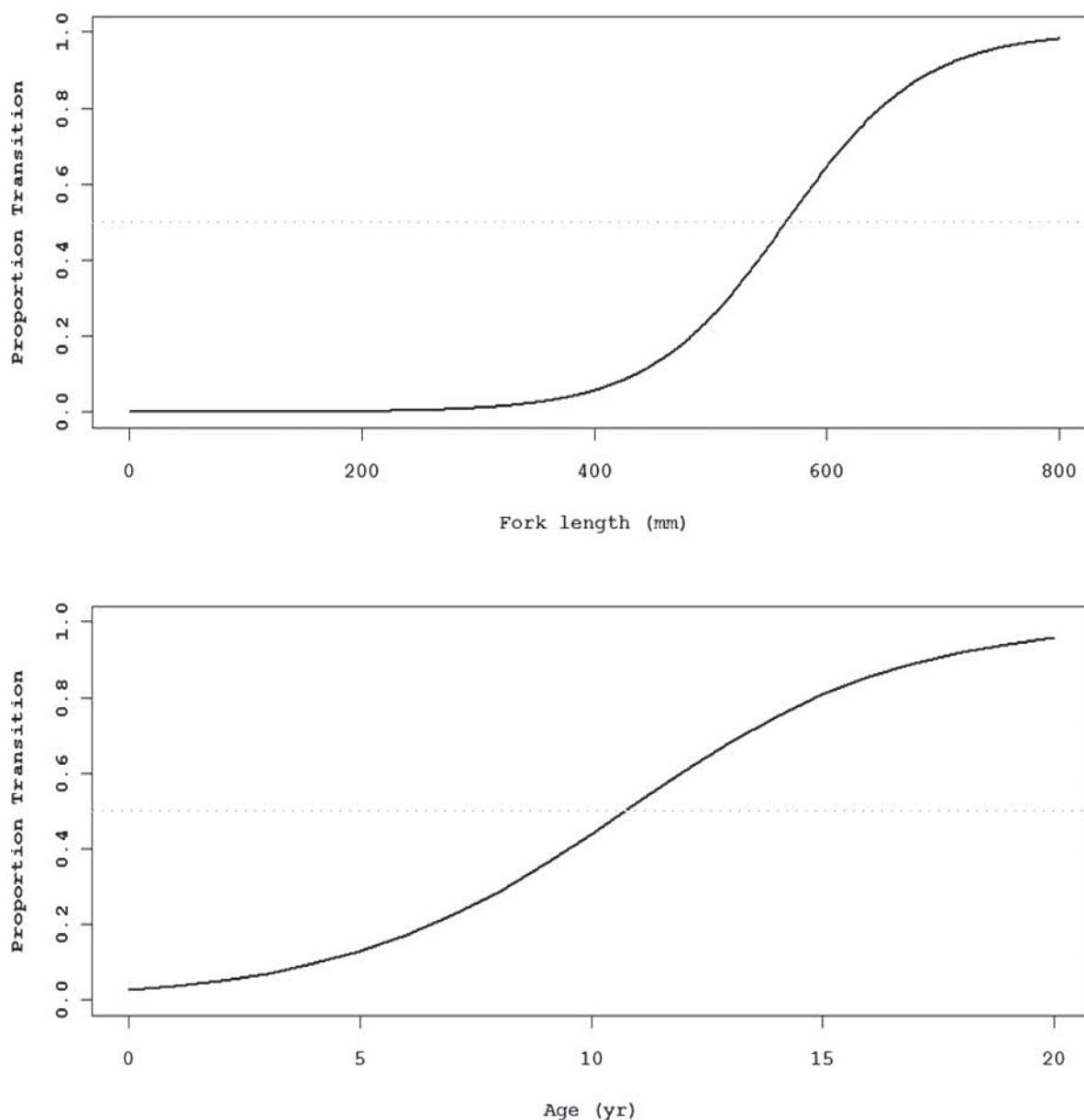


FIGURE 8. Fork length at transition (upper panel) and age at transition (lower panel; yr = years) for scamps sampled from the northern Gulf of Mexico. In both panels, the solid black line represents the logistic regression and the dashed gray line represents 50% transition (i.e., proportion of transitioned fish = 0.50).

We considered whether our reliance on fishery-dependent data was appropriate in modeling growth. Fishery-dependent data can be advantageous in that they are more generally available and are inexpensive (Begg 2005), but there are a few caveats to the interpretation of such data. The fishery effects and gear selectivity challenge the assumption that samples are representative of the population (e.g., Begg 1998). However, commercially caught scamps had normally distributed lengths. Typically, length distributions of a fishery regulated by a minimum length limit are truncated by the limit such that the distributions are skewed to the right (Harris et al. 2002; Lombardi-Carlson et al. 2008b); however, scamp modal length

in this study was about 500 mm FL, substantially larger than the commercial minimum size limit (377 mm [14.84 in] FL).

Additionally, growth models based upon fishery-dependent data warrant caution due to size limits (Haddon 2001; McGarvey and Fowler 2002). We attempted to account for the effects of the size limit on the population by fitting the von Bertalanffy growth curve using a size-modified growth model; however, modeling of scamp growth with or without the effect of a size limit resulted in similar growth parameters. Our standard and size-modified growth models predicted values for t_0 and k similar to those produced by growth models from the South Atlantic (Table 5).

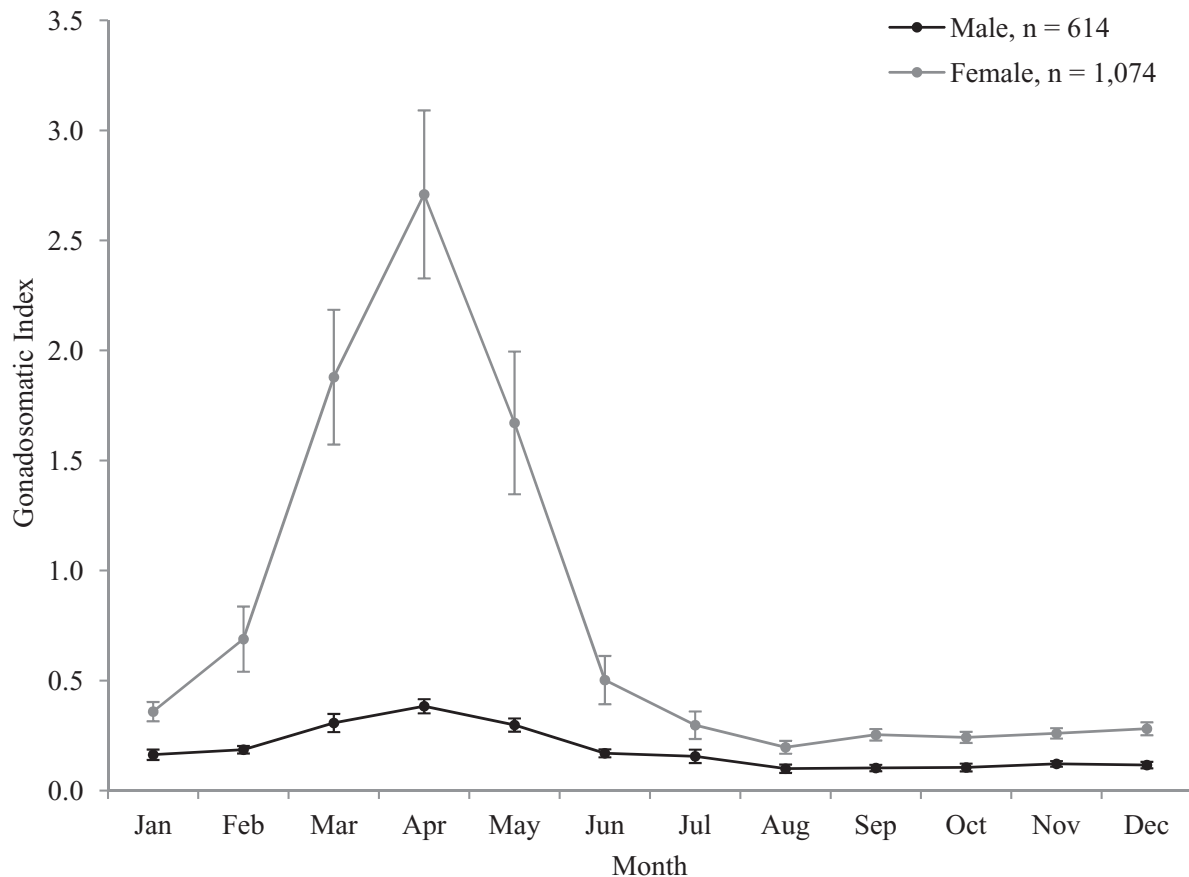


FIGURE 9. Mean (± 2 SE) gonadosomatic index by month for male and female scamps sampled from the northern Gulf of Mexico.

Therefore, we recommend that our predicted growth parameters be applied cautiously in future stock assessments.

There are a few potential explanations for why the size limit is not affecting the length of scamps in the fishery catch. First, both the state and federal size limits for scamps are based on TL, which is defined as “the straight-line distance from the tip of the snout to the tip of the tail (caudal fin), excluding any caudal filaments . . . the tail may be squeezed together to give the greatest overall measurement” (GMFMC 1999). Scamp caudal fins have elongated filaments (FMRI 1991), and if these filaments are included in the measurement of TL, the recorded length of the fish could vary tremendously. For this reason, we chose to use FL instead of TL in our analysis. Secondly, the size limit in state waters is larger than the size limit in federal waters, and 60% of the recreationally caught fish (presumably caught in state waters, 1990–2002) were below the state size limit. Possible conclusions include (1) that recreationally caught scamps were caught in federal waters or (2) that a large number of recreationally landed scamps are undersized. Finally, our data set does combine data for scamps that were landed commercially and recreationally before size limits were implemented, but length frequencies by decade were similar in distribution and average size regardless of the size limits (Lombardi-Carlson et al. 2011).

Our size-modified growth model did account for the data source (commercial or recreational) and the year of capture when assigning the size limit, but we did not account for observational errors from length measurements or the capture site’s distance from shore.

For management strategies to be successful, descriptions of age and growth are as important as descriptions of a species’ reproductive biology (Lowerre-Barbieri et al. 2011). For fish that change sex and are impacted by size-selective fishing, the removal of larger fish (i.e., males in protogynous hermaphrodites) can decrease the amount of reproductive activity due to the decrease in males, thus leading to sperm limitation, shifts in behavior, and skewed sex ratios (Armsworth 2001; Alonzo and Mangel 2004; Heppell et al. 2006). Additionally, a majority of stock assessment models use spawning stock biomass as a proxy for egg production; spawning stock biomass estimates typically only incorporate the biomass of females, but in hermaphroditic species the male biomass is just as important (Brooks et al. 2008).

Species of *Mycteroperca* have been generalized as being protogynous hermaphrodites (Hoese and Moore 1977; FMRI 1991; Harris et al. 2002), but this study is the first to provide histological evidence that scamps are protogynous hermaphrodites.

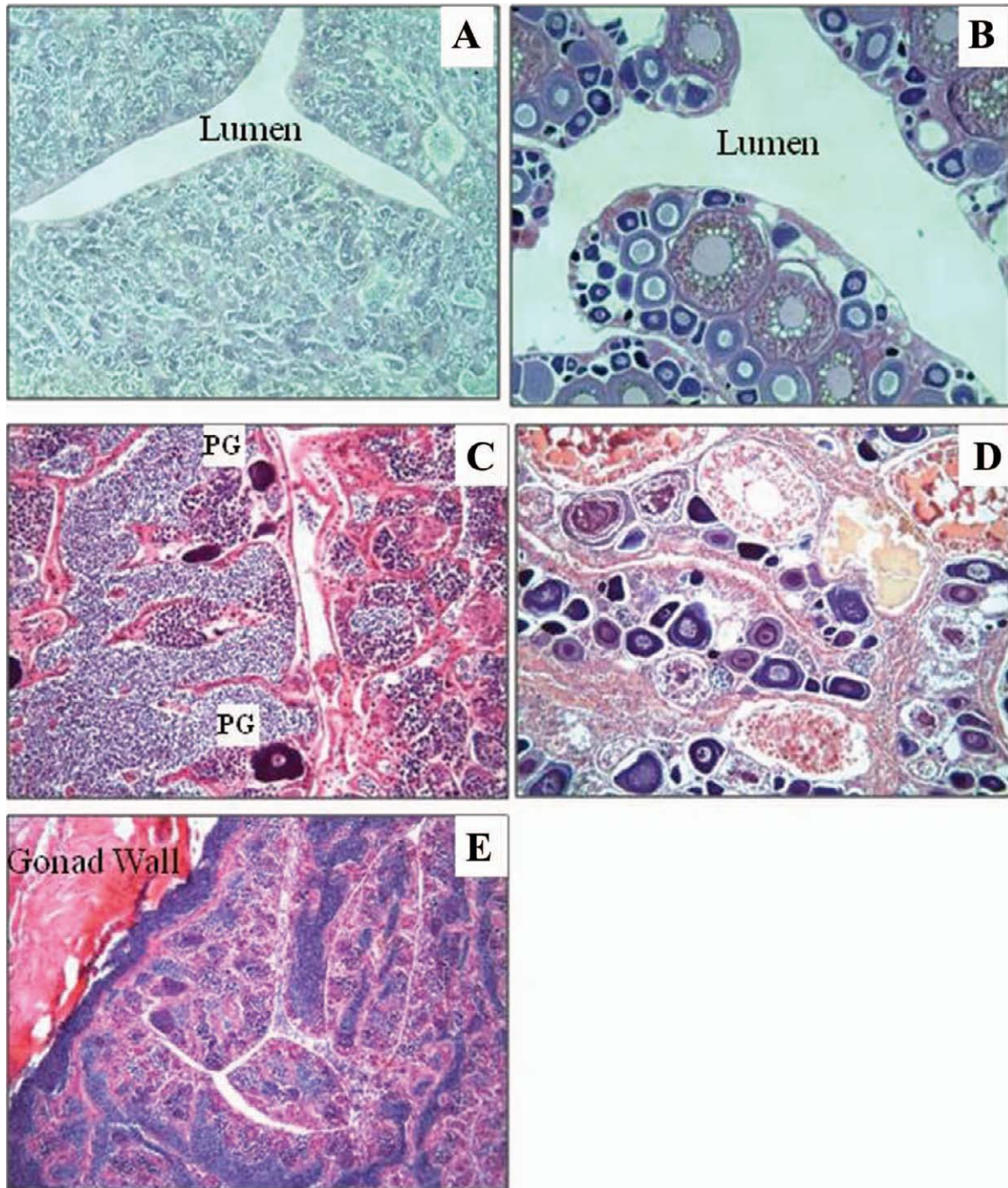


FIGURE 10. Photomicrographs of scamp histological sections: (A) membrane-lined cavity originating from the ovarian lumen in a spawning-capable male (600 mm fork length [FL], age 12; 40 × magnification) caught in February 2002; (B) membrane-lined cavity in an active, mature female (529 mm FL, age undetermined; 40 × magnification) caught in February 2002; (C) transitional individual (493 mm FL, age 11; 100 × magnification; caught in November 1979) with degenerating primary growth (PG) oocytes; (D) spawning-capable male (533 mm FL, age undetermined; 100 × magnification; caught in April 1980) with female degenerative tissue; and (E) sperm sinuses within the gonad wall of a spawning male (613 mm FL, age 16; 100 × magnification).

TABLE 5. Summary of life history parameters for scamps collected in the South Atlantic and Gulf of Mexico. Growth parameters include asymptotic length (L_{∞}), growth coefficient (k), and theoretical age at zero length (t_0) from the von Bertalanffy growth function.

Variable	Gulf of Mexico		South Atlantic	
	1972–2002	1992	1972–1979	1979–1989; 1990–1997
Collection area (and data source)	Primarily west Florida shelf (present study)	Primarily west Florida shelf (Coleman et al. 1996)	Cape Hatteras, North Carolina, to Georgia (Matheson et al. 1986)	North Carolina to Cape Canaveral, Florida (Harris et al. 2002)
Samples collected	Otoliths: $n = 6,333$ Gonads: $n = 2,481$	Gonads: $n = 150$	Otoliths: $n = 703$ Gonads: $n = 383$	Otoliths: $n = 2,573$ Gonads: $n = 2,470$
Total length (TL) or fork length (FL)	Males ($n = 801$): 221–870 mm FL Females ($n = 1,458$): 109–878 mm FL	Males ($n = 26$): 300–800 mm TL ^a Females ($n = 116$): 300–800 mm TL ^a	200–700 mm FL ^a (sex-specific values not reported)	Males ($n = 446$): 500–950 mm TL ^a Females ($n = 1,792$): 301–900 mm TL ^a
Age (years)	Males: 3–25 Females: 1–19	None provided	1–21 (sex-specific values not reported)	1–30 (sex-specific values not reported)
TL or FL at maturity	332 mm FL	None provided	None provided	1979–1989: 351–400 mm TL 1990–1997: 301–350 mm TL
Age (years) at maturity	2	None provided	None provided	1979–1989: 2 1990–1997: 1
Spawning season	Jan–Jun (peak = Apr)	Feb–Jun (peak = Apr)	Apr–Aug (peak = May–Jun)	Feb–Jul (peak = Mar–May)
Growth parameters	$L_{\infty} = 772$ mm FL $k = 0.09$ mm/year $t_0 = -4.40$ years	None provided	$L_{\infty} = 985$ mm FL $k = 0.09$ mm/year $t_0 = 2.45$ years	1979–1989: $L_{\infty} = 1,114$ mm TL $k = 0.05$ mm/year $t_0 = -7.52$ years 1990–1997: $L_{\infty} = 864$ mm TL $k = 0.12$ mm/year $t_0 = -3.15$ years

^aData summarized from tables and figures.

Histology is critical for confirming the reproductive strategy, particularly hermaphroditism (West 1990; Alonso-Fernández et al. 2011). Protogynous hermaphroditism is a type of sequential hermaphroditism in that functional female tissue is replaced by functional male tissue. Sadovy and Shapiro (1987) listed several criteria that must be observed to properly classify a fish species as a protogynous hermaphrodite. Scamps from the northern Gulf of Mexico exhibited each of those criteria. Male gonads contained a membrane-lined cavity originating from ovarian lumen, which remained unused for sperm transportation (Figure 10a). Female gonads also contained a similar membrane-lined lumen (Figure 10b). Transitional individuals, whose gonads contained degenerative ovarian tissue and developing testicular tissue (Figure 10c), had male gonads containing atretic follicles

in the testes (Figure 10d) and sperm sinuses that were present within the gonad wall (Figure 10e). Based on the work of Sadovy de Mitcheson and Liu (2008), these observations would be characterized as strong evidence for hermaphroditism in scamps. In addition to histological evidence, scamps also demonstrated sexually dimorphic growth, with males being more prevalent in the larger size-classes and older age-classes and being significantly larger at age than females. This confirms that scamps also exhibit population-level characteristics of a protogynous hermaphroditic reproductive strategy.

Describing the life history parameters of a fish species collected over several decades may be confounded by subjective and analytical biases associated with laboratory techniques, individual preferences, and computer capabilities. In our study, we

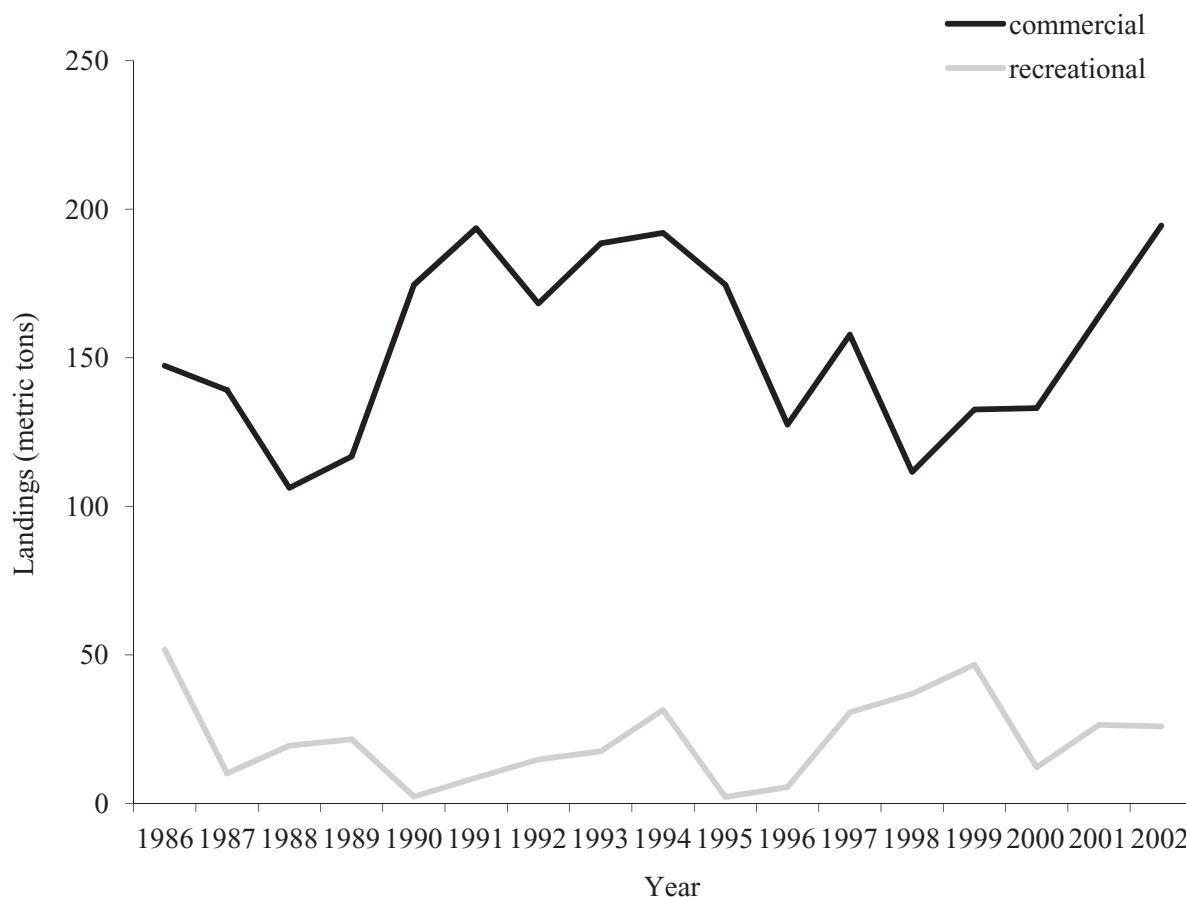


FIGURE 11. Commercial and recreational landings (1986–2002) of scamps in the northeastern Gulf of Mexico (National Oceanic and Atmospheric Administration, Fisheries Statistics Division, personal communication). Commercial landings of individual grouper species were not reported until 1986.

minimized laboratory techniques by standardizing the preparation of otoliths and gonad tissues. Only two readers interpreted the sectioned otoliths and the histologically prepared gonad tissue, and they used established guidelines and terminologies (Brown-Peterson et al. 2011). For each of these structures, the primary reader's interpretations were used in the final analysis, and we compared interreader variability to quantify any differences between individual readers. All data compilation and statistical analyses were conducted by using the same software representing the most current version available (Microsoft Office 2007; R Development Core Team 2011). Therefore, we are confident in our analysis and our description of age, growth, and reproductive life history traits for scamps collected from the northern Gulf of Mexico during 1972–2002.

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