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THE AGE AND GROWTH OF SOUTHERN FLOUNDER, *PARALICHTHYS LETHOSTIGMA,* FROM LOUISIANA ESTUARINE AND OFFSHORE WATERS

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ABSTRACT

Age and growth of southern flounder, *Paralichthys lethostigma* Jordan and Gilbert, 1884, were examined for fish sampled from Louisiana from 1987–1998. Marginal increment analysis of 1313 otolith sections verified annual opaque increment formation from January–May. Otoliths had left/right asymmetry in core position and weight. Maximum observed age for males was 4 yrs and 8 yrs for females. Total length (TL) frequency distributions were significantly different between sexes, ranging from 127–414 mm TL for males and 189–764 mm TL for females. Males had a modal TL of 280 mm, while females had a modal TL of 390 mm. No significant difference was found between inshore and offshore male TL distributions; however, females differed significantly with a higher percentage of smaller individuals offshore. Growth was significantly different between sexes and expressed with the von Bertalanffy growth equation as $L_t = 332.5\{1 - e^{[-1.03(t + 0.25)]}\}$ for males and $L_t = 556.5\{1 - e^{[-0.51(t + 0.62)]}\}$ for females. Growth parameters suggest rapid growth to age two for males and age three for females. Males exhibited a much smaller maximum theoretical size (L_∞) than females.

The southern flounder *Paralichthys lethostigma* Jordan and Gilbert, 1884 (the largest member of the family Paralichthyidae in the Gulf of Mexico; Hensley and Ahlstrom, 1984; Henderson-Arzapalo et al., 1988) is distributed from Albemarle Sound, North Carolina, to the Loxahatchee River on the lower eastern coast of Florida. The species is absent from the lower tip of peninsular Florida, but occurs from the Caloosahatchee River northward up the western coast of Florida around the Gulf of Mexico to northern Mexico (Manooch, 1984; Hoese and Moore, 1998).

The southern flounder is the most sought after flatfish along the Louisiana coast. Recreational landings in Louisiana peaked in the mid 1980s at 1362 metric tons (mt) but exhibited dramatic decreases in succeeding years; the recreational harvest fluctuated between 453 and 680 mt throughout the 1990s (Louisiana Department of Wildlife and Fisheries, 2000 southern flounder stock assessment). Commercial landings have fluctuated over the past 20 yrs, but peaked in 1994 at just below 453 mt (National Marine Fisheries Service, Fisheries Statistics and Economics Division; pers. comm.). Regulations implemented by the Louisiana State Legislature between 1995 and 1997, including a ban on set gill and trammel nets as well as the limited use of strike nets, have significantly reduced the commercial harvest in recent years. Currently a daily bag limit of ten fish per day applies to commercial and recreational fishermen. In addition, any shrimping vessel may retain and any commercial fisherman may sell all southern flounder caught as bycatch.

Age and growth studies conducted thus far have focused on southern flounder sampled from inshore estuarine locations. Stokes (1977) collected specimens from Aransas Bay, Texas and used annulus counts from whole otoliths to report a maximum age of 5 yrs, but did not validate his methods. Music and Pafford (1984) assigned a maximum age of 6 yrs to southern flounder sampled from the coastal waters of Georgia using otolith annulus counts to validate increment counts on scales. However, when evaluating the use of hard parts for age determination in southern flounder, Palko (1984) found that scales were unsatisfactory due to a lack of consistent markings. Wenner et al. (1990) estimated a maximum age of 7 yrs for southern flounder from Charleston Harbor and three nearby rivers in South Carolina, employing otolith marginal increment analysis and length frequency data to validate the periodicity of annuli in whole otoliths. Interpretations of length frequency data for validation may be suspect, however, as overlapping size classes among cohorts can complicate age-class designations (Ross, 1988). Safrit and Schwartz (1998) speared southern flounder from three locations in or near Onslow Bay, North Carolina and reported a maximum age of 7 yrs from sectioned otoliths, but did not report any validation technique. Using otolith cross-sections, Stunz et al. (2000) validated the periodicity of annulus formation by comparing mean marginal increment distances by month to report a maximum age of 4 yrs for southern flounder sampled from most major bay systems in Texas with the majority of samples from Matagorda Bay.

Southern flounder sagittal otoliths have a flat, arrowhead shape. Although growth is not uniform along all axes, the otolith grows in a radial fashion, forming adjacent opaque and translucent zones. These opaque zones may be utilized for accurate age estimation once the periodicity of zone formation has been validated (Beamish and McFarlane, 1983). Otoliths have been reported as asymmetrical in southern flounder (Wenner et al., 1990) with differences in core position between right and left otoliths, although this information has never been quantified. Otolith asymmetry was noted in numerous other flatfish species as well (Smith and Daiber, 1977; Fabre, 1988; Hovenkamp and Witte, 1991; Sogard, 1991; Haas and Recksiek, 1995). Consequently, care should be taken to recognize if such a morphological contrast exists when working with flatfish otoliths.

Previous studies noted a difference in size at age between male and female southern flounder (Gilbert, 1986; Wenner et al., 1990). Stokes (1977) stated that males grew more slowly than females and did not exceed 320 mm total length (TL), whereas Miller et al. (1991) reported a maximum size of males that was only 68% of that of females at the same age. Stunz et al. (2000) also reported that sexual dimorphism is displayed in southern flounder with males approaching a smaller theoretical maximum size at an earlier age than females.

Although southern flounder was examined throughout the southeast and Gulf of Mexico, few studies have examined both inshore and offshore life history components. The objectives of this study were to describe the age and growth of southern flounder from Louisiana inshore and offshore waters through examination of cross-sectioned sagittal otoliths, model the growth using the von Bertalanffy growth curve, and determine if southern flounder display sexual dimorphism in relation to age and growth.

Methods and Materials

Southern flounder were sampled from 1987–1998 from numerous sources with a variety of gear types. Personnel of the Louisiana State University Coastal Fisheries Institute obtained fish from commercial wholesale facilities in Grand Isle and Leeville, Louisiana in October–April 1987–1997. Inshore (estuarine) specimens were collected with gig, gillnet, and hoop net. Offshore commercial specimens were collected as by-catch from shrimp trawls from October–April, 1991–1994. Coastal Fisheries Institute personnel also obtained samples taken by hook and line from sport fishing tournaments throughout coastal Louisiana during the late spring and summer months of 1987–1996. Knowing that large fish are often entered in fishing tournaments, care was taken to obtain as many flounder as possible, not just those entered into competition. The relative locations (inshore vs. offshore) of competition specimens were not known (these fish were not

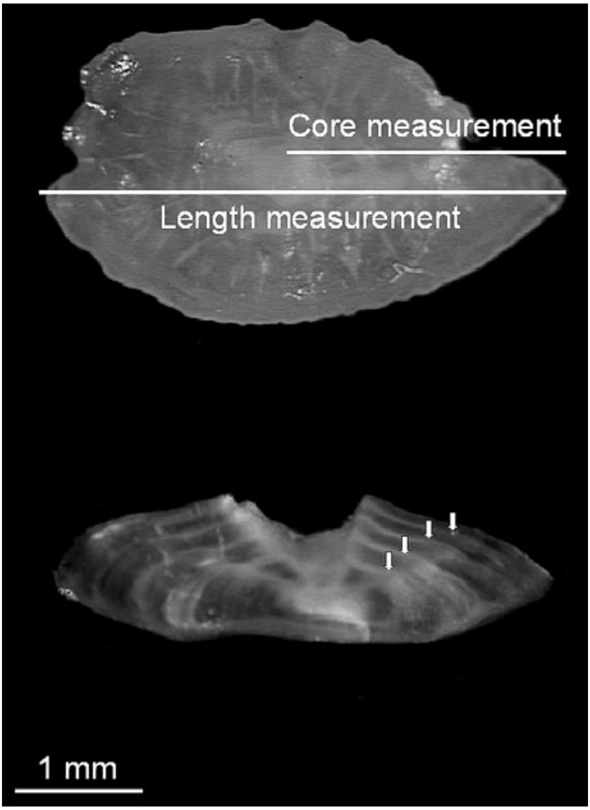

Figure 1. Photomicrographs of southern flounder sagittal otoliths under reflected light. A) Distal view of a whole otolith showing the length and core measurements. B) Photomicrograph of an otolith transverse cross-section aged at four years old. Arrows indicate opaque zones.

used in any inshore-offshore comparisons). The Louisiana Department of Wildlife and Fisheries provided inshore specimens sampled during the months of October–February of 1996 and 1997 in Barataria Bay and around Grand Terre Island with the use of gig, hook and line, pound net, and trammel net. The Louisiana Department of Wildlife and Fisheries also provided samples collected during Louisiana Offshore Oil Port (LOOP) monitoring cruises. Some samples were collected during bottom trawls and some offshore samples were trawled at 16 m (at set monitoring stations in Louisiana waters) during the months of January through June 1996. In addition, the Southeast Area Monitoring and Assessment Program (SEAMAP) provided specimens obtained from September–November 1998 with a 1.63 mm mesh, 12 m semi-ballon trawl fished in depths ranging from 1.8–40 m from randomly stratified sample locations in Louisiana waters. Specimens were weighed (total weight (TW) in g), measured (total length (TL) in mm), their gonads removed, and sex determined. Otoliths were removed and stored in ethyl alcohol until returned to the laboratory for analysis. All undamaged otoliths were cleaned of any extraneous tissue, air dried for 24 hrs, and weighed to the nearest 0.1 g.

To address the question of otolith asymmetry, a series of measurements were taken similar to those used by Haas and Recksiek (1995). A length measurement (in mm) was taken with a micrometer from the tip of the rostrum to the posterior base of the otolith, and a core measurement was taken from the center of the core to the tip of the rostrum (Fig. 1A). A core index value was then calculated by dividing the core measurement by otolith length. Differences in otolith asymmetry between sexes were examined by modeling sex specific core index – age relationships. Separate models for left and right core indices were made linear by taking the log of core index and age, and the difference between sexes was tested with an analysis of covariance (ANCOVA) and test for homogeneity of slopes on the log transformed (log[x + 1]) data. Analysis of covariance was also used on log-transformed (log[x + 1]) data to test for sex specific otolith weight – age relationships for right and left otoliths.

The left otolith of each fish was embedded in an epoxy resin and thin sectioned with a low speed saw equipped with a wafering blade (Beckman et al., 1988). Otolith cross-sections were examined with an Olympus BH-2 compound microscope with transmitted light at 40–100×. Opaque zones (annuli) were enumerated along the ventral side of the sulcul groove (Fig. 1B). Opaque zone counts were performed by two independent readers without the knowledge of capture date or sample source. Biological ages were estimated from increment count and edge condition (Beckman et al., 1991) with 1 January set as a birth date. The selection of this birth date coincided with elevated gonado-somatic indices and the presence of hydrated oocytes throughout December and January (Safrit and Schwartz, 1998) in our specimens as was reported in previous studies (Wenner et al., 1990; Stunz et al., 2000). Counting error between the two readers was evaluated after the second readings of otolith sections were completed. Reproducibility of the resultant age estimates was evaluated with the coefficient of variation, index of precision (Chang, 1982), and average percent error (Beamish and Fournier, 1981). The periodicity of opaque zone formation was examined with edge analysis and by plotting the proportion of otoliths with opaque zones at the otolith margin by month of capture (Beckman et al., 1988; Campana, 2001).

Length frequency distributions of male and female southern flounder collected in this study were examined in 20 mm TL increments to examine differences between inshore and offshore specimens and to examine the effects of gear selectivity. A Komolgorov-Smirnov two-sample test (Sokal and Rohlf, 1981) was used to test for differences between sexes and location (inshore vs. offshore). A length-weight regression was calculated on $\log_{10}$ transformed data with the model $\log_{10}$ (TW, g) = slope $\log_{10}$ (TL, mm) + intercept. Analysis of covariance (ANCOVA) and test for homogeneity of slopes were used to test for differences in regression coefficients between males and females.

Von Bertalanffy growth models of TL at age were fitted with nonlinear regression based on the formula: $L_t = L_\infty\{1 - e^{[-k(t - to)]}\}$ where t is age in years, L_t is total length at age t, L_∞ is the theoretical maximum TL, k is the growth coefficient, and t_0 is age at which TL is zero. Although the possibility exists that growth rates may change over time, we felt that it was important to combine all sampled fish from 1987–1998 in our growth models to best represent every age and size class. We combined specimens collected from offshore sources with estuarine fish when modeling growth because we believe that specimens from both relative locations do not represent distinct populations but are exhibiting different migration patterns associated with their unique life history strategy. Although southern flounder reside in estuaries throughout the year (Dahlberg, 1975), studies suggest that adults move offshore in the late fall and winter months to spawn (Ginsberg, 1952; Powell and Schwartz, 1977; Stokes, 1977; Music and Pafford, 1984; Shepard, 1986; Wenner et al., 1990). Two growth models were generated. One, three parameter (reduced) model was generated for all southern flounder of known sex; an additional six parameter (full) model was generated for all southern flounder of known sex for which models were fit independently for males and females. Each of these models also included 22 unsexed age-0 fish ranging in size from 68–214 mm TL to provide points at the lower end of the curve. A likelihood ratio test (Cerrato, 1990) was used to compare the three and six parameter models to test for differential growth between males and females. Plots of residuals were used to test for normality of the data. A significance level of 0.05 was used for all statistical analyses unless indicated otherwise.

RESULTS

In total, 1413 southern flounders (146 males, 1202 females, 22 juveniles, and 43 unknown sex) were sampled from August 1987–January 1998 for morphometric data and otoliths (Table 1). The number of fish included in the different analyses varied because not all parameters could be measured for each fish. A Kimolgorov-Smirnov two-sample test indicated a significant difference in total length-frequency distributions between

Table 1. Total number of southern flounder collected by sex (all years combined), sample source, and gear type from various sampling sources in Louisiana from 1987–1998.

Source	Gear	Males	Females	Juveniles	Unknown sex
Commercial-inshore	Gig	1	30	0	0
	Gillnet	25	324	0	3
	Hoop net	4	96	0	0
Commercial-offshore	Trawl	25	182	0	2
Fishing tournaments	Hook & line	21	410	3	27
LDWF-inshore	Gig	0	10	0	0
	Hook & line	0	5	0	0
	Pound net	11	87	0	0
	Trammel net	0	9	0	0
LOOP-inshore	Trawl	17	7	19	3
LOOP-offshore	Trawl	8	7	0	0
Seamap-offshore	Trawl	13	3	0	0
Other		21	32	0	8
Total		146	1,202	22	43

males and females (D = 83.6). Male southern flounder ranged in size from 127–414 mm TL (19–936 g TW). Males were most abundant at 280 mm with 53% of all males ranging between 260 and 300 mm TL. Males sampled from inshore waters ranged from 180–392 mm TL while those from offshore ranged from 216–385 mm TL (Fig. 2A). There was no significant difference between male inshore and offshore TL distributions (D = 23.9). Females were found at larger sizes ranging from 189–764 mm TL (61–5953 g TW). Females were most abundant at 390 mm with 53% of samples ranging from 380–440 mm TL. Female specimens sampled inshore ranged from 189–764 mm TL while offshore TLs ranged from 247–616 mm (Fig. 2B). A Kimolgorov-Smirnov test indicated a significant difference between female inshore and offshore TL-frequency distributions (D = 18.4) at 380–400 mm TL. Sex-specific length frequencies by gear are shown in Figure 3.

We found no significant differences in TL and TW relationships between sexes (ANCOVA test of homogeneity of slopes, $F_{1,\ 1235} = 0.99$; $P = 0.32$; ANCOVA test for equal intercepts, $F_{1,\ 1235} = 0.79$; $P = 0.37$). Therefore, a combined length-weight regression was fit for males and females as follows: $TW\ (g) = 3.47 \times 10^{-6}(TL^{3.21})$ ($r^2 = 0.98$, $n = 1236$).

Asymmetry was exhibited between right and left otoliths as evidenced by core index values. Right core index values ranged from 0.4–0.6 while left core indexes fell between 0.6 and 0.8. Analysis of covariance indicated no differences between sexes in core position at age for left ($F_{3,\ 286} = 0.21$, $P > 0.05$) or right otoliths ($F_{3,\ 281} = 0.03$, $P > 0.05$). A paired *t*-test indicated a significant difference between right and left otolith weights ($P < 0.0001$). Right otoliths ranged in weight from 1–340 mg while left otoliths ranged from 1–303 mg. Examination of log-transformed age-otolith weight relationships indicated a similar rate of increase in mass between sexes for left otoliths (ANCOVA test of homogeneity of slopes, $F_{3,\ 1103}$, $P > 0.05$; ANCOVA test for equal intercepts, $F_{3,\ 1103} = 29.38$, $P < 0.001$) and right otoliths (ANCOVA test for homogeneity of slopes, $F_{3,\ 1076} = 0.35$, $P > 0.05$; ANCOVA test for equal intercepts, $F_{3,\ 1076} = 15.5$, $P < 0.001$). The significance of the tests for equal intercepts for both left and right otoliths indicates that although male and female otoliths grow at the same rate, female otoliths are larger at age than male otoliths.

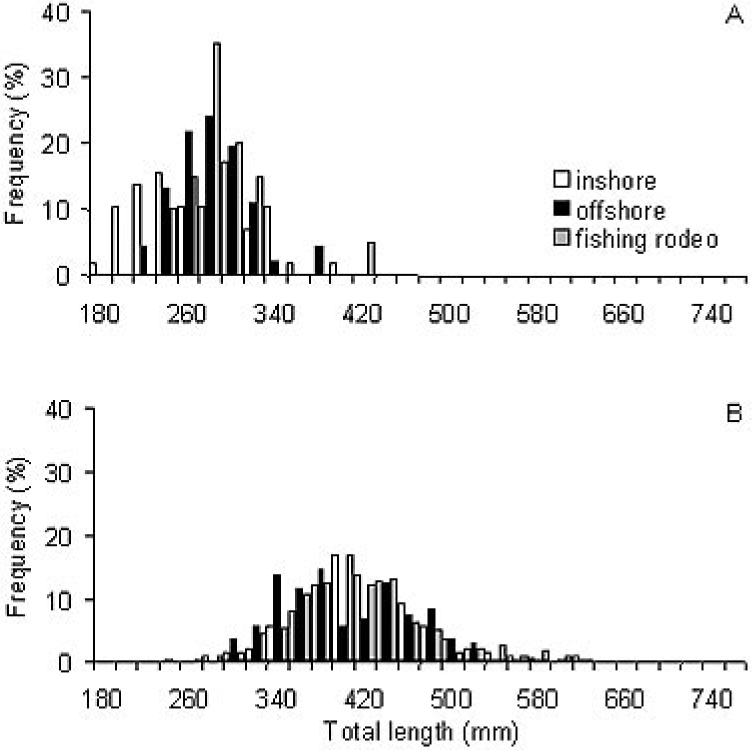

Figure 2. Total length frequency distributions of southern flounder collected from 1987–1998 (all years combined) in 20 mm increments: A) males sampled inshore (n = 58), offshore (n = 46) and at fishing tournaments (n = 21), and B) females sampled inshore (n = 570), offshore (n = 192), and at fishing tournaments (n = 410).

Opaque zones are easily distinguishable on both the ventral and dorsal sides of the sulcul groove in otolith cross-sections. Percentages of otoliths with opaque zones on the otolith marginal edge were plotted by month of capture, revealing a broad peak of individuals forming their opaque zones from January through May followed by a single extended valley indicating translucent zone formation from June through December (Fig. 4). First opaque zone formation occurred during the months of January through March in fish as small as 200 mm TL and up to 330 mm TL.

Two readers performed opaque zone counts for 1320 sampled individuals for which left otoliths were available (137 males, 1128 females, 22 juveniles, 33 unknown sex). Seven of those individuals were excluded from the analysis due to disagreement in counts between readers after two readings. Both readers agreed on all other counts (N = 1313) or 99.5% of age estimates. The average percent error was 0.5, the mean coefficient of variation was 0.0010 (0.10%) and the mean index of precision was 0.0006.

With opaque zones verified to form on an annual basis, ages were assigned ranging from 0–8 yrs (Table 2). The oldest male was sampled offshore and was aged at 4 yrs. Females reached a maximum age of 8 yrs. A Kimolgorov-Smirnov test indicated a significant difference in age structure between males and females (D = 20.7) with 22% of males aged <1 yr while only 2% of females were represented in that age class. The

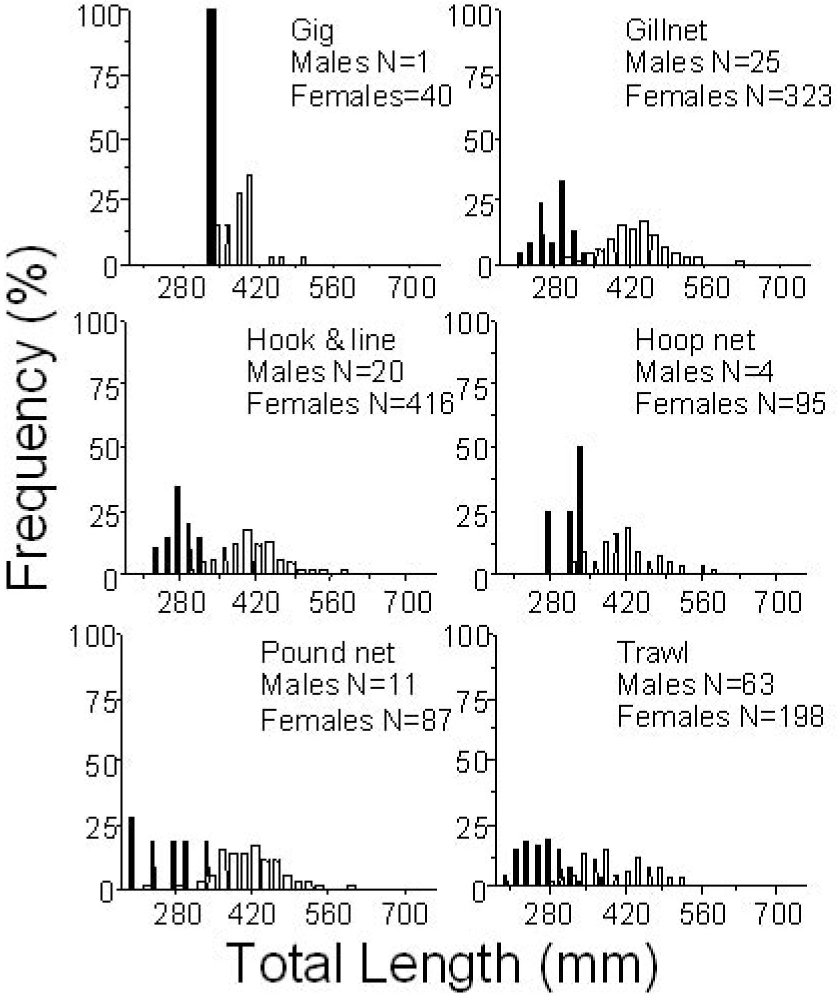

Figure 3. Total length frequency distributions in 20 mm increments by sampled gear for male (black) and female (white) southern flounder caught from 1987–1998 (all years combined). Length frequency distribution for trammel net samples not included due to low sample number (n = 10).

age structure of males did not differ between inshore and offshore populations while a significant difference was found between inshore and offshore female populations (D = 26.02) with 81% of all inshore females aged at ≤1-yr old while only 55% of offshore females were ≤ 1-yr old (Fig. 5).

Length-at-age data were fit to von Bertalanffy growth models and compared between sexes. A likelihood ratio test indicated a significant difference between the three and six parameter models indicating differential growth between males and females (χ^2 = 367.08; df = 3; N = 1276 P < 0.0001). Therefore, separate growth models were fit for each sex (Fig. 6). The von Bertalanffy growth models derived from TL are: Male: $L_t = 332.5\{1 - e^{[-1.03(t + 0.25)]}\}$ ($F_{3,155}$=123.2; P < 0.001; r^2 = 0.62) Female: $L_t = 556.5\{1 - e^{[-0.51(t + 0.62)]}\}$ ($F_{3,1139}$=22,426; P < 0.001; r^2 = 0.49).

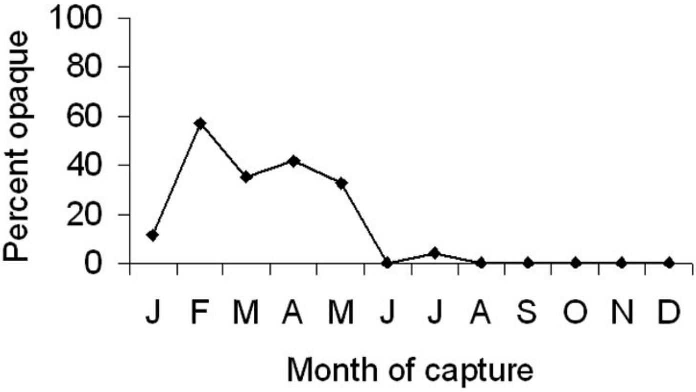

Figure 4. Marginal increment analysis of southern flounder otoliths sampled from 1987–1998 (all years combined). Percentages of opaque margin edges are plotted against month of capture.

Sex ratios were calculated by sample source and month of the year (Table 3). Females were more abundant than males in every sample source category other than LOOP and SEAMAP samples. When examining ratios by month, females outnumbered males by at least 12:1 for the months of July through January with the exception of October where females outnumbered males 4:1. In addition, the ratios of females to males from winter through spring were not quite as high at 3:1 in February, 1.5:1 in March, 7:1 in April, and 5:1 in May.

DISCUSSION

Table 2. Numbers and mean total lengths at age for southern flounder collected in Louisiana from 1987–1998.

Age (yrs)	N	Mean total length (mm)	+/- S.D.
Undetermined Sex			
0	22	129.0	40.1
Males			
0	30	256.0	21.8
1	84	271.8	43.3
2	17	317.4	34.6
3	5	302.4	17.3
4	1	374.0	
Females			
0	22	319.5	31.4
1	713	396.3	50.5
2	283	438.1	56.3
3	69	471.2	65.5
4	30	522.3	54.5
5	5	530.6	68.9
6	2	586.0	41.0
7	2	538.0	82.0
8	2	675.5	125.2

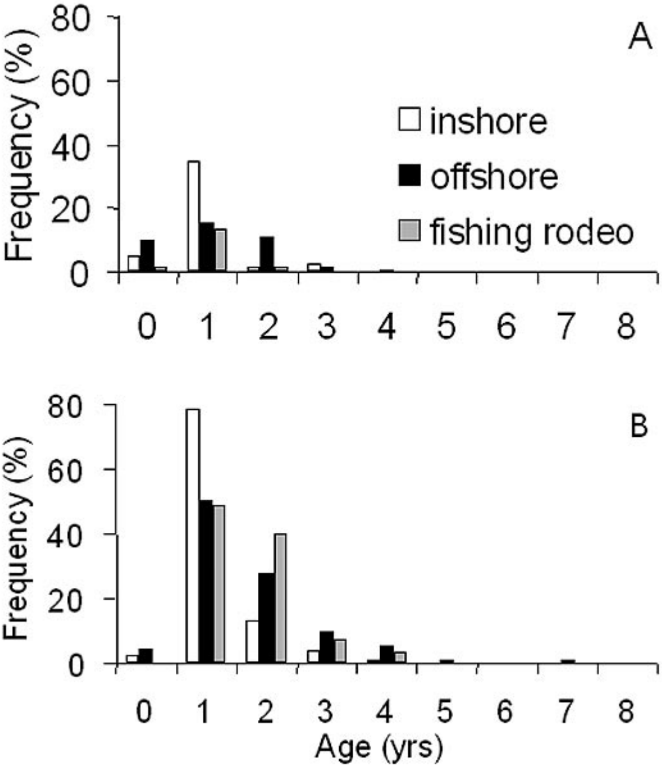

Figure 5. Age frequency distributions of southern flounder collected from 1987–1998 (all years combined) for A) males sampled inshore (n = 52), offshore (n = 46) and at fishing tournaments (n = 20), and B) females sampled inshore (n= 526), offshore (n = 191), and at fishing tournaments (n = 400).

The size structure of southern flounder in Louisiana does not appear to differ between relative inshore and offshore locations. Although juveniles were found most frequently in the estuaries, both male and female adults were distributed fairly evenly by size between inshore and offshore locations. Female inshore/offshore distributions did differ significantly with 50% of all females sampled offshore at 380 mm TL or less while only 31% of inshore females were at or below 380 mm TL, which may be attributed to gear selectivity. Most offshore fish were sampled by shrimp trawl which may target smaller individuals. Inshore specimens were collected with a number of gear types allowing for a more representative cross section of the inshore population size structure. The percentages of offshore females larger than 420 mm TL are comparable with those of inshore samples. Male length frequency distributions by relative location were similar with no significant difference found between inshore and offshore sampled populations. However smaller males were represented to a greater degree in inshore samples taken by gillnet and pound net. These two gears also appeared to select for females between 320 and 540 mm TL. Gear types such as gig and hoop net clearly showed a bias for larger individuals while hook and line samples were distributed throughout the size range of males and females.

Sex ratios were similar to those found by Music and Pafford (1984) and Stunz et al. (2000) with females found in greater numbers than males. However, the ratio of females

Table 3. Sex ratios by month (all years combined) and by sample source for southern flounder collected in Louisiana from 1987–1998.

Month	Females	Males	F/M ratio
Jan.	59	4	15:1
Feb.	36	12	3:1
Mar.	31	21	1.5:1
Apr.	27	4	7:1
May	32	6	5:1
June	13	4	3.1
July	148	5	30:1
Aug.	147	9	16:1
Sept.	78	6	13:1
Oct.	117	28	4:1
Nov.	319	33	10:1
Dec.	195	14	14:1
Source			
Commercial-inshore	450	30	15:1
Commercial-offshore	182	25	7:1
Fishing tournament	410	21	20:1
LDWF	111	11	10:1
LOOP-inshore	7	17	0.4:1
LOOP-offshore	7	8	0.9:1
SEAMAP	3	13	0.2:1

to males was not as high in offshore commercial samples. The number of females was actually less than that of males in offshore samples provided by LOOP and SEAMAP. Offshore LOOP samples taken during January–June 1996 consisted of almost equal numbers of males and females, while the inshore samples had a much higher number of males. Interestingly, with the exception of one male sampled in Little Lake northwest of Barataria Bay, all other inshore LOOP samples came from one sampling station located in lower Bayou LaFourche (29°08.30′ N, 90°13.16′ W). The greater number of males in inshore LOOP samples may be due to larger females avoiding the trawls (although equal numbers of males and females sampled from offshore LOOP trawls suggests otherwise). Their sizes (189–247 mm TL) and ages (all were aged at 1-yr old) suggest that these males may be residing in the lower part of the estuary as part of the juvenile inland phase of their life history.

The SEAMAP samples collected offshore from 30 September–19 November 1998 (at depths of 1.8–40 m) consisted of 81% males. Stokes (1977) noted that males began to migrate offshore in early October, whereas females did not begin to move offshore until November. If there is a delay in female migration offshore then one would expect to find a smaller number of females in offshore waters during this sampling period. Another interpretation of the SEAMAP ratio is the existence of more males residing offshore. Stokes surmised that older males did not return to the bays after emigration but remained in the Gulf for the duration of their lives. However, Wenner et al. (1990) suggested that no deepwater concentration of males exists due to the absence of old males in their coastal surveys (to depths of 18 m). The existence of older males residing offshore is still unknown and an increased effort to target flounder at greater depths may be warranted.

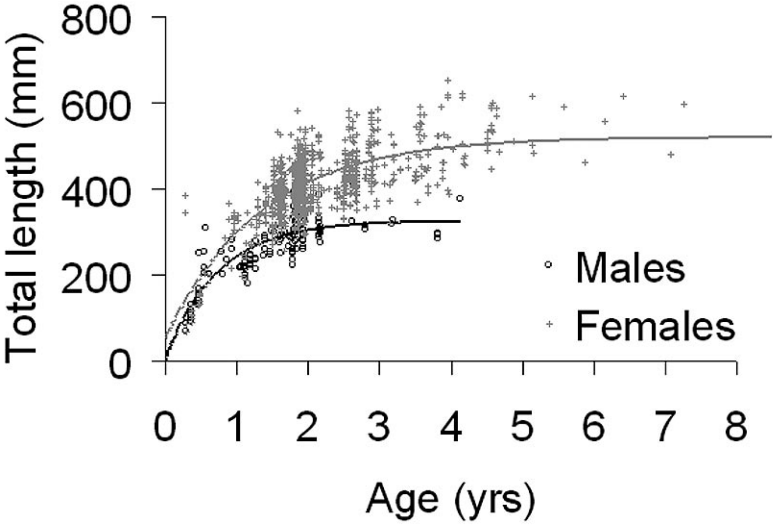

Figure 6. Von Bertalanffy growth models fitting total length-at-age for male and female southern flounder sampled from 1987–1998 (all years combined). Each model includes 22 unsexed juveniles ranging from 68–214 mm.

When examining sex ratios by month, the decrease in numbers of females:males in October may indicate the suggested early migration of males through the estuaries to spawn offshore followed by female migration offshore in November and December. The higher number of females to males from July–September must be attributed to the majority of samples collected from hook and line fishing tournaments that target individuals (primarily females). Therefore little information can be gleaned from those ratios.

Southern flounder otoliths are generally flat in comparison to the curved, crescent shape found in many other marine teleosts. Although both right and left otoliths may be used for age estimation, they display asymmetry in the position of the core and in weight. This otolith asymmetry is evident by the time southern flounder reach 68 mm TL (the smallest specimen in our analysis) and warrants the consistent use of the right or left when using otoliths for age estimation or dealing with flatfish otolith measurements to reduce variation.

Otolith marginal increment analysis supports the assumption that one opaque zone is accreted on the otolith between the months of January–May followed by translucent zone formation from June–December. Thus, opaque zones on sectioned otoliths may be utilized for accurate yearly age estimation (Barger, 1985). The maximum monthly percentage of 56% of southern flounder with an opaque zone at the growing edge of the otolith is consistent with the findings of Beckman and Wilson (1995) who, in a review of 49 studies of northern hemisphere temperate fish populations using sectioned otoliths, reported a maximum mean monthly percentage of 65% of individuals with an opaque zone at the growing edge of the otolith.

Analysis of sectioned otoliths of age-0 and yearling southern flounder indicated first opaque zone formation as early as 200 mm and up to 330 mm TL. First opaque zone formation began in January with all yearlings completing their first opaque zone by March. Stokes (1977) reported lengths of up to 300 mm TL by first opaque zone formation in southern flounder; Wenner et al. (1990) detected no delayed or "lost" first annulus.

Therefore, variability in size at formation of the first opaque zone is most likely attributed to differential growth among individuals, which Fitzhugh et al. (1996) stated as an explanation for the broad dispersion of lengths occurring in the first year.

Female southern flounder live longer than males, reaching a maximum age of 8 yrs while males reached only 4 yrs. The two females aged at 8 yrs came from an offshore charter boat trip and from a hook and line tournament, both targeting larger, presumably older fish. Our maximum ages are consistent with previous studies (Wenner et al., 1990; Safrit and Schwartz, 1998), but varied from those of Stunz et al. (2000) who found maximum ages of 4 yrs for both males and females. Stunz et al. focused on inshore sampling using similar gear (hook and line, gill and trammel nets, and gig) as this study and suggested that older flounder probably occur.

The age structure of females was significantly different across the depth gradient with only 19% of all inshore females aged at ≥2 yrs while 45% of females sampled offshore were aged at ≥2 yrs. Given that most offshore samples were collected during the months of December and January when southern flounder are known to move offshore to spawn (Stokes, 1977; Shepard, 1986; Henderson-Arzapalo et al., 1988; Wenner et al., 1990), and because females become reproductively mature by age two (Stokes, 1977; Safrit and Schwartz, 1998), it is not entirely surprising that a higher percentage of older females was found offshore. A higher proportion of older males were sampled offshore with 35% aged at ≥2 yrs compared with only 10% of inshore males aged at ≥2 yrs. Again, this may be attributed to the increased offshore sampling effort during the southern flounder-spawning season when older individuals relocate to offshore waters.

Growth parameters suggest rapid growth to age two for males and age three for females. Each sex-specific growth model included 22 age-0 fish of undetermined sex ranging from 68–214 mm TL. Difficulty in determining sex at these small sizes has been previously noted. Music and Pafford (1984) stated that sex could not be determined before 130 mm for females or 232 mm for males while Stokes (1977) maintained that sexual differentiation was not possible for either sex before 170 mm. Due to the capacity of juvenile southern flounder for high growth rate relative to other fishes (Fitzhugh, 1993), the addition of these individuals into each growth model, in effect, pulled the curve toward zero resulting in a higher growth coefficient (k), which more accurately predicted growth of southern flounder in the first few years of life.

This study also predicts smaller maximum sizes for males and females than previously reported (Wenner et al., 1990; Matlock, 1992). Maximum theoretical size was calculated at 332.5 and 556.5 mm TL for males and females, respectively. The increased number of large individuals in our sample population forced the asymptote of the growth curve down and thus, to a smaller theoretical maximum size. The absence of such individuals in a sample population would result in an elevated maximum size. Such was the case when Matlock (1992) reported a maximum theoretical size of 848 mm TL from a data set of only 21 southern flounder ranging from 250–560 mm TL.

Questions remain regarding the differing life history patterns of male and female southern flounder. The apparent under-representation of males in this study may be due to the difficulty in obtaining males at greater depths offshore. Future research must include a concerted sampling effort to target individuals offshore and to examine if southern flounder stratify themselves at different depths by age, sex, and size. Additional research such as mapping strontium-calcium ratios in otolith chemistry may also provide insight as to where both males and females reside throughout their lives. A growing number of studies suggests discriminate growth between males and females. Do larger, older males exist and if so, where are they located? Examination of these questions is of critical importance to fully understand the complex life history strategy of this species.

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