The Life History of Southern Flounder (Paralichthys Lethostigma) in Louisiana Waters

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THE LIFE HISTORY OF
SOUTHERN FLOUNDER (PARALICHTHYSS LETHOSTIGMA)
IN LOUISIANA WATERS

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
In partial fulfillment of the
Requirements for the degree of
Master of Science

in

The Department of Oceanography and Coastal Sciences

by

Andrew James Fischer
B.S., Louisiana State University, 1995
May 1999
MANUSCRIPT THESES

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# Table of Contents

Acknowledgements.......................................................................................................... ii  
List of Tables.................................................................................................................... v  
List of Figures................................................................................................................... vi  
Abstract............................................................................................................................ viii  
Introduction....................................................................................................................... 1  
Methods and Materials................................................................................................... 12  
  Age and Growth...................................................................................................... 13  
  Reproductive Biology............................................................................................. 17  
Results............................................................................................................................. 25  
  Meristic data........................................................................................................... 25  
  Age and Growth...................................................................................................... 29  
  Reproductive Biology............................................................................................. 38  
Discussion........................................................................................................................ 50  
  Meristic Data.......................................................................................................... 50  
  Age and Growth..................................................................................................... 52  
  Reproductive Biology............................................................................................. 54  
Conclusions..................................................................................................................... 61  
Literature Cited................................................................................................................. 63  
Vita................................................................................................................................... 68
List of Tables

1. Estimated maximum age for male and female southern flounder in the Atlantic and northern Gulf of Mexico. Method of age estimation and sample location are included ...........................................................10

2. Numbers of southern flounder collected by various sampling sources from 1987 to 1998. Sample numbers have been separated by sex ......................26

3. Mean batch fecundity estimates for female southern flounder sampled during the 1991 and 1993 spawning seasons. Minimum and maximum numbers of ova per batch are also reported. Estimation of individual batch fecundity of 8 female southern flounder (4 in 1991 and 4 in 1993) was assessed as a mean of twelve estimates from each individual. Two replicate samples were taken from the anterior, medial, and posterior regions of each lobe of the gonad ............................................................................43

4. Comparison of spawning frequency estimates for female southern flounder sampled during the 1991-92 and 1993-94 spawning seasons using the postovulatory and time-calibrated methods. Day-0 females (imminent spawners) are evidenced by the presence of late vitellogenic oocytes and day-1 (recent spawners) are those exhibiting POFs ........................................................................................................45

5. Maximum likelihood estimates calculated for female southern flounder sampled during 1987-1998 spawning seasons. Fifty percent and one hundred percent maturity schedules were calculated. Estimates were calculated for total length and total weight ........................................................................46

6. Sex ratios of southern flounder sampled from 1987 to 1998 by month of the year. Samples taken in fishing tournaments were not included because of possible bias due to fishing location ........................................................................47

7. Sex ratios of southern flounder sampled from 1987 to 1998 by sample source ........................................................................................................48
List of Figures

1. Photograph of southern flounder, *Paralichthys lethostigma* ........................................... 2

2. Distribution of southern flounder in the United States. Southern flounder range from Albemarle Sound NC, to the Loxahatchee River on the lower eastern coast of Florida. It is absent on the southern peninsular tip of Florida but occurs in the Caloosahatchee River and up the western coast of Florida around the Gulf of Mexico to Northern Mexico ............................................. 3

3. Photomicrograph of southern flounder right sagittal otolith lying concave (distal) side up...................................................................................................................... 9

4. Photomicrograph of southern flounder sagittal otolith lying concave (distal) side up, the rostrum pointing to the right. Core and length measurements were taken from sagittae to calculate core index values. Core measurement divided by the length measurement = core index value ............................................................................. 14

5. Photomicrograph of a transverse section near the core of a southern flounder otolith. Arrows point to opaque zones or “annuli” which are counted for age estimation ........................................................................................................ 16

6. Photograph of a southern flounder ovary. Each ovary consists of two lobes each divided into three regions: A) anterior, B) medial, and C) posterior for a total of six regions per ovary ............................................................................................................. 19

7. Photomicrographs at 100x magnification of oocytes at the various stages of maturation; (A) primary growth, (B) cortical alveolar, (C) vitellogenesis, and (D) hydration. Arrows indicate each cell stage ....................................................................................................................................... 20

8. Photomicrograph of histologically prepared ovary tissue sample containing a postovulatory follicle (POF) taken at 100x magnification. Arrow indicates postovulatory follicle location .............................................................. 22

9. Length frequency distribution of male, female and juvenile southern flounder caught from 1987 to 1998. Males range in size from 68mm to 414mm and are most abundant at 280mm interval. Females range in size from 189mm to 764mm and are most abundant at 390mm interval. Juveniles range from 68 to 309mm and were most abundant at 100mm interval Males are shown in shaded pattern, females are shown in white, and juveniles are shown in solid black ..................................................................................................................... 27

10. Length frequency plots of SEAMAP and LOOP data. LOOP length frequency data from the years 1978 to 1995 were combined. SEAMAP data includes all occurrences of southern flounder in the Gulf of Mexico from 921 stations ............................................................................................................. 28
11. Length-weight regression on log_{10} transformed data for male and female southern flounder from 1987 to 1998

12. Plot of core index values of left and right sagittal otoliths demonstrating the asymmetry with position of the core between right and left otoliths. Nearly all right core index values fell between 0.4 and 0.6 while the majority of left core index values fell between 0.6 and 0.8. The large black cross indicates the plotted right core index of a reversed southern flounder. The right core position is similar to the left core position of normal flounder.

13. Marginal increment analysis of southern flounder sagittal otoliths sampled from 1987 to 1998. Percentages of opaque and translucent margin edges are plotted against month of the year to indicate time of annulus formation. Opaque zones were found between the months of January and May and the margins of nearly all samples were translucent from August through December.

14. Plot of otolith edge condition of 1285 southern flounder sectioned sagittal otoliths sampled from 1987 to 1998. The plot of edge condition shows the progression of opaque zones from January through May and translucent zones from March through December.

15. Monthly length-frequencies of young-of-the-year (uncheckered) and yearling southern flounder sampled from 1987 to 1998 to show progression of first annulus formation. Yearlings without an opaque ring on their otolith are shown in black, those with an opaque ring are shown in checkered pattern. The x-axis is total length (mm) and the y-axis is number of fish.

16. Age frequency distribution for male and female southern flounder sampled from 1987 through 1998. Males reached a maximum age of 4 years and females reached a maximum age of 8.5 years.

17. Von Bertalanffy growth models fit for male and female southern flounder sampled from 1987 through 1998. Each model includes 22 unsexed individuals ranging from 68mm to 214mm.


19. Monthly mean gonadosomatic indices plotted by month of the year for male (N = 113) and female (N = 1090) southern flounder sampled from 1987 to 1998. Male indices are represented by the circular dotted line and female indices by the square dotted line.

20. Plot of monthly percent oocyte stages from 386 female southern flounder sampled from 1987 to 1998; PG (primary growth), CA (cortical alveolar), V (vitellogenic), and H (hydrated). Percentages are plotted from July through June to demonstrate the progression of oocyte maturation with the onset of the spawning season.
Abstract

The objectives of this study were to describe the life history patterns of the southern flounder (Paralichthys lethostigma) in Louisiana waters through determination of age, growth, and reproductive biology. A variety of sample sources were included to demonstrate how the southern flounder life cycle is dependent on both the estuary and offshore waters throughout the various stages of its life cycle.

Females exhibited greater lengths then males reaching a maximum of 764mm total length and males a maximum of 414mm. Ages were estimated through examination of transverse sections of sagittal otoliths. Annuli were validated to form yearly in the winter months. Females lived longer then males reaching a maximum age of eight years while males reached a maximum of 4 years. Resultant Von Bertalanffy growth equations were shown to be significantly different between males and females. Males displayed a higher growth rate then females but had a much smaller L∞.

Histological evidence and gonadosomatic indices indicate that southern flounder spawn in December and January in offshore waters. Southern flounder are batch spawners indicated by the presence of multiple stages of oocytes throughout the spawning season. Mean batch fecundity was estimated for 1991 and 1993 as 62,000 and 44,000 ova per batch. Spawning frequency was estimated using the postovulatory follicle method as 3.6 days and 6.4 days. The time-calibrated method provided estimates of 2.3 days and 3.1 days. Females were found to reach fifty-percent maturity at 229mm and all females were mature above 509mm.

Sex ratios indicate that males begin to migrate offshore as early as October in preparation for the spawning season. Female migration offshore takes place in
November and December. Both males and females begin to move back into the estuaries as early as February as the spawning season comes to an end.
Introduction

The southern flounder, *Paralichthys lethostigma*, is the largest member of the family Paralichthyidae (Hensley et al. 1984) in the Gulf of Mexico (Henderson-Arzapalo et al. 1988) (Figure 1). Southern flounder is an important species throughout the region. Commercial and recreational landings of *Paralichthys* along Louisiana coasts for 1997 were estimated to be 94,898 lbs. and 319,607 lbs. (personal communication from the National Marine Fisheries Service, Fisheries Statistics and Economics Division). It is the dominant targeted flatfish in the region and based on life history and distribution of the other two congener species, it is safe to assume that the great majority, if not all of the flatfish catch, is *lethostigma* (Dr. Bruce A. Thompson, Coastal Fish. Inst., LA State Univ., Baton Rouge, pers. commun). The southern flounder is fished in Louisiana mainly using hook and line, gigging, and by trawl.

Life history studies on southern flounder are scant and have been conducted in South Carolina (Wenner et al. 1990), Georgia (Music and Pafford 1984), and in Texas (Stokes 1977). Nall (1979) reported data on Alabama and Florida panhandle fish. These and other studies have been summarized in several species profiles compiled on southern flounder including Adkins et al. (1996) in Louisiana, Gilbert (1986) in south Florida, and Reagan and Wingo (1985) in the Gulf of Mexico. However, little is known of its life history in Louisiana waters.

Southern flounder are distributed from Albemarle Sound, North Carolina, to the Loxahatchee River on the lower eastern coast of Florida. They are absent on the southern peninsular tip of Florida, but occur in the Caloosahatchee River and up the western coast of Florida and around the Gulf of Mexico to northern Mexico (Hoese and Moore 1998, Manooch 1984) (Figure 2). Southern flounder have been captured offshore of Alabama, Mississippi, and Louisiana from the barrier islands to the outer
Figure 1. Photograph of southern flounder, *Paralichthys lethostigma*. 
Figure 2. Distribution of southern flounder in the United States. Southern flounder range from Albemarle Sound NC, to the Loxahatchee River on the lower eastern coast of Florida. It is absent on the southern peninsular tip of Florida but occurs in the Caloosahatchee River and up the western coast of Florida around the Gulf of Mexico to Northern Mexico.
shelf, and on the inner shelf from Apalachee Bay to above Tampa Bay, Florida (Reagan and Wingo 1985).

Southern flounder have been reported in a small number of studies throughout its range. From spring through fall southern flounder are found along shorelines of bays, lagoons, sounds, and river systems in relatively shallow water (Ginsburg 1952, Gutherz 1967) and are most commonly found in the mid to upper reaches of estuaries, occasionally entering fresh water (Dahlburg 1975, Ginsburg 1952). Southern flounder prefer substrates of clayey silt or rich organic muds, which may account for the absence of the species on the southern peninsular tip of Florida. Southern flounder are frequently found in low salinity estuarine areas (Powell and Schwartz 1977) and have been reported to be euryhaline collected from waters ranging in salinity from 0 to 36 (Stokes 1977). Southern flounder have been taken by gigging along the Mississippi River for considerable distances above the mouth (Ginsburg 1952). They have also been taken by hoop net seventy miles up the Mississippi River in Port Hudson in the commercial catch of blue catfish and seined from the Alabama River as far north as Claiborne (Dr. Bruce A. Thompson, Coastal Fish. Inst., LA State Univ., Baton Rouge, pers. comm.). Southern flounder have also been found in the Alabama River below Claiborne Lock and Dam (river mile 117.5) setting a new inland record for the species in Alabama (Mettee et al. 1996).

Adults exhibit a late fall migration offshore to spawn (Ginsburg 1952). Stokes (1977) found a similar migration out of Aransas Bay into the Gulf of Mexico from mid-October through mid-December with maximum migration in mid-November. He stated that this movement coincided with a rapid water temperature decrease of about 4°C to 5°C. Stokes also noted that males began to migrate offshore before females, evidenced by the absence of males in estuarine samples after late November. Shepard (1986) reported on the spawning peak of southern flounder in Louisiana and
stated that “Emigration of adult flounders in late fall and winter, and their subsequent capture through shrimping activity in the Gulf indicates that spawning occurs in offshore waters.” Powell and Schwartz (1977) reported that adult southern flounder do not move offshore until just prior to spawning after which they return to inshore waters. Stokes (1977) found adults began to reenter Aransas Bay as early as February.

Juveniles begin to move inshore in late winter. The main period of recruitment to the estuary nursery grounds occurs in January and peaking in March (Wenner et al. 1990). Wenner et al. (1990) reported a major ingress of 1cm young of the year into South Carolina’s estuarine creeks in January and found a few individuals of the same size in the creeks as late as April. Stokes (1977) also found that migration of juveniles into Aransas Bay began in January but found February to be the maximum month of movement into the estuaries. The mechanism of southern flounder ingress is similar to many late-winter, early-spring estuarine immigrants. Weinstein et al. (1980) reported that post-larval *Paralichthys* species in the Cape Fear River estuary settled at the bottom of estuarine creeks during ebb tide and rose in the water column during flood tide resulting in a net up-estuary transport. Deubler (1960) showed that survival of early post-larval southern flounder was not affected by salinity lower than 26, but when food supply, temperature, and light were controlled, growth was faster at higher salinities. Fitzhugh (1993) reported that age-0 flounder are found in estuarine waters of all depths, but were the only age class to be found in areas less than 1.8 m deep. He also stated that larger individuals of an age-0 cohort were found in deeper water then smaller individuals (Fitzhugh 1993).

It appears that a number of flatfish exhibit sexual dimorphism in age and growth rates. Solomon et al. (1987) found that the growth of male and female *Limanda yokohamae* differed; females exhibited a higher growth rate than males of the same age. The same observation was reported for stone flounder, *Kareius bicoloratus*
(Uehara and Shimizu 1996) with females reaching a greater size and living longer. Lux (1973) reported that female winter flounder, *Pleuronectes americanus*, grew faster than males after the second year. Lux and Nichy (1969) also stated a similar pattern of growth in the New England yellowtail flounder, *Limanda ferruginea*. Gilbert (1986) reported that there is evidence that *Paralichthys* females reach a larger size than males. Stokes (1977) stated that male southern flounder grew slower than females and did not exceed 320mm total length where Miller et al. (1991) reported a difference in maximum size between male and female southern flounder with male maximum size at only 68% of females at the same age. Therefore, it may be critical to generate separate growth curves by sex to properly manage the fishery.

Commercial landings for southern flounder in Louisiana have fluctuated since the 1950s with the highest landings in the mid-1990s at 0.97 million pounds (Louisiana Department of Wildlife and Fisheries 1998). Substantial restrictions have been put on the southern flounder fishery in recent years leading to a decrease in commercial landings. Commercial harvest methods were changed in 1995 with the passage of Act 1316 of the 1995 Regular Legislative Session, the Marine Resources Conservation Act of 1995 outlawing the use of set gill nets and trammel nets (Louisiana Department of Wildlife and Fisheries 1998). This act also limited the harvesting of southern flounder by the use of strike nets to a period of the third Monday of October to March 1 of the following year. The act required a “restricted species permit” to harvest flounder in Louisiana waters. By March 1, 1997 all harvest by gill and trammel nets was banned.

Additional regulations were put into place on the recreational and commercial fisheries on March 1, 1996. These regulations limited the number of southern flounder to 10 fish per boat and one days limit in possession for recreational fishermen and a limit of ten flounder per person aboard a commercial vessel. Changes were made again with Acts 1163 and 1352 of the 1997 Regular Legislative Session allowing
commercial and recreational fishermen to have the daily limit of 10 fish in their possession for each day that they were on the water. In addition, a limit of 100 pounds of southern flounder was put into place for commercial shrimping vessels.

Proper management of a species depends upon accurate age and growth estimates. It is essential to obtain the age structure of the fish populations being harvested to effectively monitor the status of those stocks (Williams and Bedford 1974). Age and growth information is used to calculate growth parameters with the use of the Von Bertalanffy growth model. These parameters are applied to population dynamics models such as the Beverton-Holt model which calculates maximum sustained yield; the maximum amount of exploitation of a fishery in which the stock can recover to healthy levels.

The age structure and longevity of a species is important in formulating a management strategy. Short-lived species can recover more rapidly from overexploitation due to a lower age at maturity. However, overfishing of numerous age classes including juveniles and adults could reduce the numbers of individuals to critically low levels. Although long-lived species often have a higher age at maturity and a greater number of age classes in the spawning population, overexploitation of the spawning stock would require a longer recovery time in order to return to healthy levels. The age at which a species reaches maturity is also essential in setting effective size restrictions to ensure a healthy spawning stock.

Age estimation can be accomplished through a variety of techniques. Tag and recapture studies and analysis of hard parts such as spines, scales and otoliths can be used to estimate age. When evaluating the use of hard parts to determine age in southern flounder, Palko (1984) found that although otoliths and vertebrae were both useful in determining age, scales were unsatisfactory due to a lack of consistent
markings. Otoliths are the preferred method of determining age due to their easy removal in the field with minimal damage to the fish.

The sagitta, the largest of the three pairs of teleost otoliths is arrowhead shaped in the flounder (Figure 3). Although growth of the otolith is not uniform along all axes, it grows in a radial fashion forming layers of opaque and translucent zones. These zones, or annuli, are often utilized for age estimation; but in order to do so, the periodicity of the annuli must be validated. Validation of this periodicity of annuli formation is as important in fisheries biology as standardizing solutions or calibrating instruments are in other sciences (Beamish and McFarlane 1983).

Sagittal otoliths were reported to be asymmetrical in southern flounder (Wenner et al. 1990) although this information has never been quantified. Otolith asymmetry has also been noted in Paralichthys dentatus (Smith and Daiber 1977), Paralichthys isosceles (Fabre 1988), plaice Pleuronectes platessa (Hovenkamp and Witte 1991), as well as in the winter flounder Pseudopleuronectes americanus (Haas and Recksiek 1995). It is therefore important to understand the morphological contrast between the left and right sagitta when dealing with flatfish otoliths (Sogard 1991).

The few studies conducted on the age and growth of southern flounder suggest that they are a short-lived species (Table 1). Nall (1979) reported a maximum age of 10 years using whole otoliths, but did not validate his methods. Stokes (1977) used whole otoliths and reported a maximum age of 5 years for southern flounder. Wenner et al. (1990) used whole otoliths and reported a maximum age of 7 years using length frequency data and marginal increment analysis to validate the use of whole sagittal otoliths. Interpretation of length frequency data for validation may be suspect, however, because overlapping size classes of cohorts beyond two years (Ross 1988) can complicate age-class designations. Music and Pafford (1984) assigned a maximum age of 6 years using scales. They attempted to use otolith counts to
Figure 3. Photomicrograph of southern flounder right sagittal otolith lying concave (distal) side up.
Table 1. Estimated maximum age for male and female southern flounder in the Atlantic and northern Gulf of Mexico. Method of age estimation and sample area are included.

<table>
<thead>
<tr>
<th>Area</th>
<th>Method(1)</th>
<th>Max Male Age</th>
<th>Max Female Age</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Texas</td>
<td>O</td>
<td>3</td>
<td>5</td>
<td>Stokes 1977</td>
</tr>
<tr>
<td>Alabama &amp; Florida</td>
<td>O</td>
<td>-</td>
<td>10</td>
<td>Nall 1979</td>
</tr>
<tr>
<td>Georgia</td>
<td>S</td>
<td>3</td>
<td>6</td>
<td>Music &amp; Pafford 1984</td>
</tr>
<tr>
<td>South Carolina</td>
<td>O</td>
<td>3</td>
<td>7</td>
<td>Wenner et al. 1990</td>
</tr>
</tbody>
</table>

(1) Method O = whole otolith, S = scale
document the validity of increment counts on scales, although it is unclear whether they used whole or sectioned otoliths.

Little information is known about southern flounder reproductive biology and spawning activity. Spawning season duration and maturity schedules have been reported by Shepard (1986), Stokes (1977), and Wenner et al. (1990) although none of these authors used histological evidence to describe reproductive activity. Fecundity estimates have been reported by Arnold et al. (1977), Henderson-Arzapalo et al. (1988), and Laswell et al. (1978) on southern flounder reared in aquaculture studies, but no estimates have been calculated for southern flounder spawning in their natural environment. The offshore spawning pattern of southern flounder makes it difficult to obtain samples during the spawning season. Offshore samples are essential in obtaining a true picture of southern flounder reproductive biology.

There is a lack of age, growth, and reproductive biology data for southern flounder in the state of Louisiana and in the Gulf of Mexico. This data is essential in understanding the status of the fishery stock and in creating a successful management plan. The objectives of this study are to describe the life history pattern of southern flounder in Louisiana waters through examination of age and growth and the reproductive biology of the species. Growth will be modeled using the Von Bertalanffy growth curve. Males and females will be compared to determine if southern flounder displays sexual dimorphism in age and growth and if separate models are required. Reproductive development will be examined to determine southern flounder spawning season and duration, weight and length at sexual maturity, annual and batch fecundity, and spawning frequencies.
Methods and Materials

Southern flounder used in this study came from a variety of sample sources from Louisiana waters or the Gulf of Mexico off the coast of Louisiana. Multiple sources provided the most reasonable cross section of the estuaries near shore population. Samples were collected at commercial docks in Grand Isle and Leeville LA from October 1997 to January 1998 (n = 146). The Louisiana Department of Wildlife and Fisheries at the St. Amant Marine Laboratory also collected samples from Grand Terre with the use of a pound net during from November and December 1997 (n = 125). An existing flounder data set compiled by Dr. Bruce Thompson of the Coastal Fisheries Institute of Louisiana State University was also used in the analysis (n = 1134). This data set contains samples from 1987 to 1998 from a variety of sources with the large majority from commercial fish docks (n = 565) and hook and line fishing rodeo tournaments (n = 421). I intended to acquire offshore fish samples during the spawning season with the help of local fishermen, but due to the heavy regulations and restrictions placed on the fisheries, a feeling of distrust towards management has resulted. This feeling of distrust prevented me from identifying a cooperative fisherman willing to allow me to accompany him offshore.

Fish were weighed (mg), measured (total and standard lengths in mm), sex determined, and gonads and sagittal otoliths removed. Gonads were stored under ice and returned to the laboratory where they were cleaned of any extraneous tissue, weighed, and preserved in 10% buffered formalin. Sagittal otoliths were removed in one of two ways. The first was to make a horizontal cut just above the eye back to the preopercle. A vertical cut is then made removing a triangular section of the head exposing the labrynth containing the otoliths. The second method was to remove the gills and cut through the skull, exposing the labrynth. This method is preferred when sampling a commercial catch as it minimized visible damage to the fish. Sagittae were
removed with forceps from the labyrinth. Otoliths were stored in ethyl alcohol to preserve until they were returned to the laboratory for analysis.

Otoliths were cleaned of any extraneous tissue and air dried for at least twenty-four hours. Right and left otoliths were then weighed (+/- 0.01 mg). A length measurement of the whole otolith was taken from the tip of the rostrum to the base of the otolith (in mm) using a micrometer under a dissecting microscope. A core measurement, from the center of the core to the rostrum of the otolith, was also taken (Figure 4). A core index value was calculated by dividing the core measurement into the otolith length. Haas and Recksiek (1995) used similar measurements in the determination of otolith asymmetry in winter flounder. Core index readings for right and left otoliths were then plotted against fish length.

A length – weight regression was calculated on log_{10} transformed data using the model \( \log_{10} (\text{weight, g}) = \text{slope} \log_{10} (\text{TL, mm}) + \text{intercept} \). Linear regressions were also calculated for otolith weight (mg) – age using the model otolith weight = age (slope) + intercept. Analysis of Covariance was used to compare sexes for both regressions.

**Age and Growth**

Fish were aged in the Coastal Fisheries laboratory through processing and analysis of 1286 sagittal otoliths. A number of fish in the data set were not aged due to missing or broken sagittae. Due to the morphological differences between right and left saggitae, The left was chosen for embedding. Otoliths were placed horizontally lying concave side up, rostrum pointing to the left into a vertical embedding cup. Once the otoliths were positioned correctly, an embedding mixture of five parts araldite 8702 epoxy resin to one part hardener 8700 was poured into the cups to cover the otoliths. The resin was left to harden for twenty-four hours. Once the material hardened, the block of resin containing otolith was removed from the cup and each otolith block
Figure 4. Photomicrograph of southern flounder sagittal otolith lying concave (distal) side up, the rostrum pointing to the right. Core and length measurements were taken from sagittae to calculate core index values. Core measurement divided by the length measurement = core index value.
labeled with the appropriate identification number. Each block was mounted onto the Beuhler Isomet low-speed saw and positioned so that the anterior/posterior axis of the otolith is perpendicular to the saw blade. Two transverse sections near the core of the otolith were taken and glued on to glass slides. The better of two sections was polished and inscribed with an identification number, and aged. Otolith sections were analyzed and ages assigned with the use of Olympus BH-2 compound microscope with BH2-RFL reflected light fluorescence. Sections were read along the medial side of the section along the ventral side of the sulcus groove (Figure 5).

Reader variability was also evaluated; otoliths were viewed and aged by each of two independent readers without the knowledge of the date of capture or sample source. Ages were assigned based on annulus count and edge condition. Edge condition was recorded as opaque or translucent using the criteria of Beckman et al. (1991) as follows: opaque edges were coded as “1” indicating the opaque zone was up to 1/3 complete; “2” if the opaque zone was between 1/3 and 2/3 complete; and a code of “3” if the opaque zone was 2/3 to fully complete. Translucent edges were coded as “4” indicating the translucent zone was up to 1/3 complete; “5” if the translucent zone was between 1/3 and 2/3 complete; or “6” if the translucent zone was 2/3 to fully complete. Opaque and translucent zone completion was based upon comparison of the width of the proceeding opaque or translucent zone. Ages were assigned based on a January 1 birth date from Wenner et al. (1990) and data from this study.

Marginal increment analysis and a plot of edge condition by month were used to determine the periodicity of annulus formation in southern flounder otoliths. In addition, length-frequency distributions were plotted by month for young of the year (YOY) and yearlings with and without opaque zones on their otoliths to determine age of first annulus formation.
Figure 5. Photomicrograph of a transverse section near the core of a southern flounder otolith. Arrows point to opaque zones or "annuli" counted for age estimation.
Length frequency distributions were examined for males and females of this study as well as for length frequency data obtained by Louisiana Offshore Oil Port (LOOP) and Southeast Area Monitoring and Assessment Program (SEAMAP). Distributions were plotted in 20mm intervals. LOOP length frequency data from 1978 to 1995 were combined. SEAMAP data includes all occurrences of southern flounder in the Gulf of Mexico from 921 stations. A Kolmogorov-Smirnov two-sample test (Tate and Clelland 1957) was used to test for differences between sexes and LOOP and SEAMAP length frequencies. Sex ratios were calculated by sample source and by month of the year.

Sex specific Von Bertalanffy growth equations were derived from total lengths using nonlinear regression (SAS Institute Inc., 1985) based on the formula:

\[ L_t = L_\infty \left( 1 - e^{-(k(t-t_0))} \right) \]

where \( t \) is age in years, and \( L_t \) is total length at age \( t \), \( L_\infty \) is the theoretical maximum length, \( k \) is the growth coefficient, and \( t_0 \) is age at which length is zero. Individual fish were not included in the analysis if age or length data was not available. Each model also included 22 unsexed juveniles to provide points at the lower end of the curve. These juveniles ranged in size from 68mm to 214mm total length.

The resultant models fitting parameters for both males and females were then combined into one full six-parameter model and compared to a reduced model on the pooled data in which sex was not considered. A likelihood ratio test of the six-parameter and the pooled data models was used to test for differences in the models. Plots of residuals were used to test for normality of the data.

Reproductive Biology

The reproductive biology of southern flounder was examined using several indices to determine spawning season duration, maturity schedules, and estimate
batch and total fecundity. Gonadosomatic indices (GSI) were calculated and used to
document the expression of gonad weight as a function of body size (Htan-Han 1978).
GSI was calculated using the following equation:

\[\text{GSI} = 100 \times \frac{\text{Gonad weight (wet wt blotted dry)}}{\text{Body weight (total wt - viscera and gonads)}}\]

A representative gonad tissue sample was taken from all individuals sampled
during the spawning season (n = 323) to determine the stage and rate of maturation of
oocytes. This random tissue sample was selected from one of six regions of the gonad
(two lobes containing anterior, medial, and posterior regions) (Figure 6). The tissue
sample was placed in an omnisette tissue cassette and processed by the LSU School
of Veterinary Medicine, Department of Pathology where it was embedded in Paraplast
(Sherwood Medical Industries), sectioned, stained with Gill hematoxylin, and
counterstained in eosin Y. Oocyte stages were described following Wallace and
Selman (1981) as:

1. Primary Growth Phase (P.G.) (Figure 7a). Cytoplasm is very basophilic and has
large nucleus to cytoplasm ratio. There may be several large nucleoli present near the
periphery of the lightly stained nucleus. Cytoplasm becomes less basophilic as the cell
grows and cell size range overlaps the following stage. Late follicle consists of primary
oocyte surrounded by a layer of squamous cells.

2. Cortical Alveolar (CA) (Figure 7b). Cytoplasm is less basophilic during this stage and
follicle is identified by the appearance of “yolk vesicles” that increase in size and
proliferate throughout the cytoplasm. Nucleus stains more darkly than previous stage.

3. Vitellogenesis (V) (Figure 7c). Dark acidophilic yolk globules appear signaling the
uptake of vitellogenin (yolk protein) accounting for the great size range within this
stage. Cytoplasm is moderately basophilic in the beginning periods of this stage as
seen in the previous stage and membrane-bound peripheral yolk spheres. As cell
Figure 6. Photograph of a southern flounder ovary. Each ovary consists of two lobes each divided into three regions: A) anterior, B) medial, and C) posterior for a total of six regions per ovary.
Figure 7. Photomicrographs at 100x magnification of oocytes at the various stages of maturation; (A) primary growth, (B) cortical alveolar, (C) vitellogenesis, and (D) hydration. Arrows indicate each cell stage.
continues to grow, yolk spheres proliferate and increase in size. Late stages of vitellogenesis show transition to next stage with coalescence of yolk and enlargement of oocyte.

4. Hydration (H) (Figure 7d). Nuclear membrane becomes less evident as the nucleus migrates towards the animal pole and yolk vesicles begin to coalesce in the early phase of hydration. Coalescence continues and cytoplasm takes on a smooth appearance as oocyte enlarges. Maximum size before ovulation is reached and cell takes an irregular shape or collapse due to preservation and sectioning.

5. Postovulatory Follicle (POF) (Figure 8). Following ovulation/spawning, the follicle collapses into the opening left behind by the shed hydrated oocyte. Cytological proof that spawning has taken place. They are characterized by a highly vascularized thecal layer and distinctive granulosa cells and are reabsorbed by the fish probably within one to two days.

Oocytes were counted by microscopic examination of prepared slides at 40X or 100X magnification with the use of BioScan OPTIMAS image processing software and the Optimas imaging system. Fields were randomly chosen to stage approximately 200 oocytes per section. An oocyte was not counted unless at least 50% of the cell was visible in the field (Brown-Peterson et al. 1988, Fitzhugh et al. 1988). Each slide was also scanned two to three times for atretic oocytes and postovulatory follicles. Degrees of atresia were assigned following Hunter and Macewicz (1985).

Batch fecundity was estimated on eight females with hydrated oocytes (4 in 1991 and 4 in 1993) using the hydrated oocyte method of Hunter et al. (1985). Two replicate tissue samples weighing approximately 30-50mg each were taken from the six regions of the ovary (for a total of twelve replicates per female). Each sample was placed on a slide and covered with a few drops of glycerin. The oocytes in the sample were then gently loosened with forceps and spread over the slide, and hydrated.
Figure 8. Photomicrograph of histologically prepared ovary tissue sample containing a postovulatory follicle (POF) taken at 100x magnification. Arrow indicates postovulatory follicle location.
oocytes were microscopically counted. Batch fecundity was calculated as (number of hydrated oocytes/sample weight) * gonad weight. An analysis of variance (ANOVA) was applied to the samples to determine if there were significant differences between ovarian lobes, among ovarian regions, or between the replicate samples taken.

Spawning frequency was estimated using two different methods after histological examination of all ovaries collected during the spawning season (n = 323). The postovulatory follicle method (Hunter and Goldburg 1980, Hunter and Macewicz 1985, Hunter et al. 1986, Nieland and Wilson 1993, 1994) takes the proportion of females with POFs (and have just spawned) out of the number of mature females in the sample to obtain a spawning fraction. The spawning fraction is inverted to obtain the spawning frequency, the average number of days that lapse between spawning events. The “time-calibrated” method includes imminent spawners as well as fish that have just spawned to determine spawning frequency (Brown-Peterson et al. 1988, Fitzhugh et al. 1993, Nieland and Wilson 1994). Proportions of day-0 spawners (imminent spawners evidenced by the presence of late vitellogenic oocytes) and day-1 spawners (recent spawners evidenced by the presence of POFs) in the female spawning population are calculated. An average of the two proportions gives the spawning fraction. This spawning fraction is inverted as well to obtain the spawning frequency. In both methods, the presence of vitellogenic oocytes was used as criterion for determination of maturity in females. All postovulatory follicles were assumed to be less then 24 hours old based on the description of the degeneration of northern anchovy postovulatory follicles described by Hunter and Macewicz (1985). Ovaries exhibiting signs of alpha or beta atresia were not used in the calculations since these individuals have effectively left the spawning population and the probability of future spawning during the season is zero (Hunter and Macewicz 1985). Annual fecundity
(AF) was then estimated as $AF = (\text{spawning season} \ [\text{days}] / \text{spawning frequency} \ [\text{days}]) \times \text{batch fecundity}$ (Nieland and Wilson 1993).

Maturity schedules were determined by length and weight using maximum–likelihood analysis (PROBIT) in Statistical Analysis System (SAS Institute Inc., 1985) (Nieland and Wilson 1993). Maturity by length was calculated by comparing the number of mature females in 10mm intervals with the total number of females in each length interval. The same comparison was made with 100mg intervals to determine maturity schedules by weight. A significance level of 0.05 was used in all statistical tests unless otherwise noted.
Results

Fourteen hundred and five southern flounders (139 males, 1201 females, 22 juveniles, and 43 unsexed) were sampled from August 1987 through January 1998. Fish came from numerous sources including commercial and recreational catches from the northern Gulf of Mexico, Louisiana Offshore Oil Port (LOOP) trawls, and the Louisiana Department of Wildlife and Fisheries which provided samples of flounder taken from Barataria Bay (Table 2). The varieties of sample sources are necessary to illustrate how the southern flounder life cycle is dependent on the estuaries and offshore waters for the various stages of its life cycle. Because not all parameters could be measured for each fish, the numbers of fish included in the different analyses vary.

Meristic Data

Total length (TL) frequency distributions plotted by sex were significantly different (p < 0.05) (Figure 9). Males ranged in size from 68mm to 414mm TL. Males were most abundant at the 280mm interval with fifty-three percent of all males ranging from 260mm to 300mm TL. Females were more abundant at much larger sizes ranging from 189mm to 764mm TL and were most abundant at the 390mm interval. Fifty-three percent of all females ranged from 380mm to 440mm TL. As expected, males also had a much lower range in body weight then females ranging from 19g to 936g. Females ranged in weight from 61g to 5953g.

Length frequency distributions for SEAMAP and LOOP data were significantly different (p < 0.05) (Figure 10). In addition, each data set was found to be significantly different from both the male and female distributions of this study (p < 0.05). SEAMAP length frequency peaked at 280mm total length with forty-two percent of individuals ranging between 260 and 300mm total length. LOOP length frequency had a mode of
Table 2. Numbers of southern flounder collected by various sampling sources from 1987 to 1998. Sample numbers have been separated by sex.

<table>
<thead>
<tr>
<th></th>
<th>Females</th>
<th>Males</th>
<th>Juveniles</th>
<th>Unsexed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Commercial</td>
<td>384</td>
<td>38</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Commercial-Offshore</td>
<td>131</td>
<td>22</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Hook and Line Tournament</td>
<td>403</td>
<td>18</td>
<td>3</td>
<td>27</td>
</tr>
<tr>
<td>LOOP Trawls</td>
<td>14</td>
<td>24</td>
<td>19</td>
<td>3</td>
</tr>
<tr>
<td>Hoop Net</td>
<td>126</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>LDWF</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Other</td>
<td>31</td>
<td>19</td>
<td>0</td>
<td>8</td>
</tr>
</tbody>
</table>
Figure 9. Length frequency distribution of male, female and juvenile southern flounder caught from 1987 to 1998. Males range in size from 68mm to 414mm and are most abundant at 280mm interval. Females range in size from 189mm to 764mm and are most abundant at 390mm interval. Juveniles range from 68 to 309mm and are most abundant at 100mm interval. Males are shown in shaded pattern, females are shown in white, and juveniles are shown in solid black.
Figure 10. Length frequency plots of SEAMAP and LOOP data. LOOP length frequency data from 1978 to 1995 were combined. SEAMAP data includes all occurrences of southern flounder in the Gulf of Mexico from 921 stations.
240mm total length with forty-four percent of individuals ranging between 220 and 260mm total length.

Regression equations of log_{10} transformed data were calculated to predict total weight at total length for males and females (Figure 11). Analysis of covariance (ANCOVA) showed no statistical difference between sexes (p > 0.05 for slopes; p > 0.05 for intercepts). Therefore, a combined length–weight regression was fit for males and females:

\[
\log_{10} \text{weight (g)} = 3.21 \log_{10}(\text{TL, mm})-5.46 \quad (r^2 = 0.98) \quad (n = 1236).
\]

The slope of 3.21 was significantly different then 3 (p < 0.0001).

**Age and Growth**

Southern flounder sagittae are arrowhead shaped and generally flat in comparison to the crescent like shape of sagittae in many other marine species. The center of the otolith has an opaque core surrounded by alternating translucent and opaque rings. I had suspected that the right and left otoliths were asymmetric with position of the core. Core index values demonstrate this asymmetry (Figure 12). Most right core index values fell between 0.4 and 0.6 while nearly all left core index values fell between 0.6 and 0.8. The graph contains the plotted right core index of a reversed southern flounder. This southern flounder reversed at metamorphosis lying on its left side rather than its right. The right core position is similar to the left core position of normal flounder. A core index value could not be calculated for the left otolith because it had already been processed before this analysis began.

Opaque rings are easily distinguishable on both the ventral and dorsal sides of the sulcus groove in cross section of southern flounder otoliths. Marginal increment analysis and a plot of otolith edge condition were used to determine the seasonal
Figure 11. Length-weight regression on log_{10} transformed data for male and female southern flounder from 1987 to 1998.
Figure 12. Plot of core index values of left and right sagittal otoliths demonstrating the asymmetry with position of the core between right and left otoliths. Nearly all right core index values fell between 0.4 and 0.6 while the majority of left core index values fell between 0.6 and 0.8. The large black cross indicates the plotted right core index of a reversed southern flounder. The right core position is similar to the left core position of normal flounder.
periodicity of annulus formation. Opaque margins were found in fish caught from the
months of January and May and the margins of nearly all samples taken from August
through December were translucent (Figure 13). The plot of edge condition
corresponded with marginal increment analysis showing the progression of opaque
zones from January through May and translucent zones from March through December
(Figure 14). Length-frequency distributions for young of the year (YOY) and yearlings
indicated first annulus formation as early as 200mm in length and up to 330mm (Figure
15). The first annulus appeared on YOY otoliths between the months of January and
March.

Ages were assigned through analysis of 1285 sagittae. Seven sagitta were
excluded from the analysis due to lack of agreement between the two readers. Each of
the seven age estimates differed by one year. The two readers agreed on all other
otolith annulus counts (N = 1279) or 99.5% of age estimates. The mean coefficient of
variation (V) was 0.0011. The mean index of precision (D) was 0.00081 indicating an
average error of 0.08 annuli per one hundred counts (Beckman 1989).

A large number of the fish collected were estimated to be two years of age
(Figure 16). Forty-six percent of females and thirty-six percent of males fell into this
age class. The oldest female was 8.5 years in age and the oldest male was found to
be 4.13 years.

Data were fit to Von Bertalanffy growth model and compared. A likelihood ratio
test indicated that there was a significant difference between a full six-parameter Von
Bertalanffy growth model and the pooled data growth model (p <0.0001). Therefore,
separate growth models were fit for each sex (Figure 17). The Von Bertalanffy growth
models derived from total lengths are:

\[ \text{Male} \quad L_t = 325.65 \left\{ 1 - e^{-1.33(t - 0.01)} \right\} \quad (r^2 = 0.68) \]
Figure 13. Marginal increment analysis of southern flounder sagittal otoliths sampled from 1987 to 1998. Percentages of opaque and translucent margin edges are plotted against month of the year to indicate time of annulus formation. Opaque zones were found between the months of January and May and the margins of nearly all samples were translucent from August through December.
Figure 14. Plot of otolith edge condition of 1285 southern flounder sectioned otoliths sampled from 1987 to 1998. The plot of edge condition shows the progression of opaque zones from January through May and translucent zones from March through December.
Figure 15. Monthly length-frequencies of young-of-the-year (uncheckered) and yearling southern flounder sampled from 1987 to 1998 to show progression of first annulus formation. Yearlings without an opaque ring on their otolith are shown in black, those with an opaque ring are shown in checkered pattern. The x-axis is total length (mm) and the y-axis is number of fish.
Figure 16. Age frequency distribution for male and female southern flounder sampled from 1987 through 1998. Males reached a maximum age of 4 years and females reached a maximum age of 8.5 years.
Figure 17. Von Bertalanffy growth models fit for male and female southern flounder sampled from 1987 through 1998. Each model includes 22 unsexed individuals ranging from 68mm to 214mm.
Female \( L_t = 520.14 \left(1 - e^{0.74(t + 0.14)}\right) \) \((r^2 = 0.52)\)

Plots of residuals indicated normal distribution of the data.

Right otoliths ranged in weight from 1 to 340mg while left otoliths ranged from 1 to 303mg. A paired \( t \)–test indicated a significant difference between right and left otolith weights \((p < 0.0001)\). Furthermore, an Analysis of Covariance indicated a significant difference between right otolith weight and sex \((p < 0.0001)\) and left otolith weight and sex \((p < 0.0001)\). Therefore, regressions were run for right and left otolith weight by age for males and females:

Male  
\[
\text{Age} = 0.034(\text{right otolith weight (mg)}) + 0.75 \quad (r^2 = 0.44)
\]
\[
\text{Age} = 0.038(\text{left otolith weight (mg)}) + 0.63 \quad (r^2 = 0.51)
\]

Female  
\[
\text{Age} = 0.022(\text{right otolith weight (mg)}) + 0.70 \quad (r^2 = 0.62)
\]
\[
\text{Age} = 0.024(\text{left otolith weight (mg)}) + 0.58 \quad (r^2 = 0.62)
\]

Left otolith weight provided higher \( r^2 \) values for males. The relationship between left otolith weight and age is shown in Figure 18.

Reproductive Biology

Gonadosomatic indices and ovarian histology indicate that southern flounder spawning season lasts approximately 60 days from December through January. Monthly mean GSI data provides evidence of the annual spawning cycle (Figure 19). A slight increase in GSI for both sexes occurred in October followed by more dramatic increases in November and December. Maximum GSI levels for both sexes occurred in December and January and declined by March.

An annual cycle of oogenesis and recrudescence is also displayed in a plot of monthly percent oocyte stages in southern flounder ovaries (Figure 20). Primary growth oocytes made up virtually all oocytes in samples from April through September. Cortical alveolar oocytes reached highest levels in October and decreased to minimum
Figure 18. Plot of relationship between left otolith weight and age for male and female southern flounder sampled from 1987 through 1998.
Figure 19. Monthly mean gonadosomatic indices plotted by month of the year for male (N = 113) and female (N = 1090) southern flounder sampled from 1987 to 1998. Male indices are represented by the circular dotted line and female indices by the square dotted line.
Figure 20. Plot of monthly percent oocyte stages from 386 female southern flounder sampled from 1987 to 1998; PG (primary growth), CA (cortical alveolar), V (vitellogenic), and H (hydrated). Percentages are plotted from July through June to demonstrate the progression of oocyte maturation with the onset of the spawning season.
levels by March. Vitellogenic oocytes began to appear in October and reached maximum proportions in November and December; coinciding with minimum proportions of primary growth oocytes. Hydrated oocytes were found only in December and January. Postovulatory follicles were found in individuals caught on December 12 and 13, 1991 and December 17 and 20, 1993. One additional female was found with postovulatory follicles on 28 January 1994. Females began to show signs of atresia stage 1 (< 50 % of yolked oocytes in alpha stage of atresia) (Hunter and Macewicz 1985) in mid-to-late January. Oocytes reached atresia stage 3 (> 50% of yolked oocytes in alpha stage of atresia) by February.

Batch fecundity was determined for 8 females (4 in 1991 and 4 in 1993) with hydrated oocytes. An ANOVA indicated there was a significant difference in hydrated oocyte distribution between ovarian lobes (p < 0.05) and regions within lobes (p < 0.05) indicating southern flounder ovaries are not homogenous. Therefore, estimation of individual batch fecundity should be calculated from samples from various regions of the ovary. Batch fecundity was estimated as the mean of 12 estimates calculated for each fish (two replicate samples from the anterior, medial, and posterior regions of each lobe of the gonad). Fecundity ranged from 46,046 to 71,680 ova per patch in 1991 and from 14,046 to 68,736 ova per batch in 1993. Mean batch fecundities were significantly different between years, but this is likely insignificant due to the small number of samples for each year. Mean batch fecundity by year was 62,473 in 1991 and 44,225 in 1993 (Table 3). A linear regression and LSD and Duncan’s multiple range tests showed that there is a significant difference between mean batch fecundity for the two years (p < 0.0001). Linear regression indicated no correlation between batch fecundity and total length (p > 0.05), total
Table 3. Mean batch fecundity estimates for female southern flounder sampled during the 1991 and 1993 spawning seasons. Minimum and maximum numbers of ova per batch are also reported. Estimation of individual batch fecundity of 8 female southern flounder (4 in 1991 and 4 in 1993) was assessed as a mean of twelve estimates from each individual. Two replicate samples were taken from the anterior, medial, and posterior regions of each lobe of the gonad.

<table>
<thead>
<tr>
<th>Year</th>
<th>1991</th>
<th>1993</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Batch Fecundity</td>
<td>62,473</td>
<td>44,225</td>
</tr>
<tr>
<td>Min/Max</td>
<td>46,457 – 71,680</td>
<td>14,046 – 68,736</td>
</tr>
</tbody>
</table>
weight (p > 0.05), eviscerated weight (p > 0.05), gonad free body weight (p > 0.05), or age (p > 0.05).

Spawning frequency estimates using the postovulatory method ranged from one spawning event every 2.9 to 4.8 days in the 1991 spawning season, and one event every 5.3 to 12.5 days in the 1993 spawning season (Table 4). The time-calibrated method produced similar estimates between years with one spawning event every 2.9 days in the 1991 spawning season and one spawning event every 3 to 6.3 days in 1993. The estimates derived from the time-calibrated method seem more plausible in comparison to published spawning frequencies of species such as the black drum and red drum where spawning frequency was calculated as one spawning event every two to four days (Fitzhugh et al. 1993, Nieland and Wilson 1993, 1994).

Annual fecundity estimates were calculated using mean annual batch fecundity estimates and spawning frequencies from the postovulatory and time-calibrated methods. Annual fecundity based on spawning frequencies derived from the postovulatory follicle method ranged from 787,474 to 1,292,544 ova in 1991 and from 212,280 to 504,467 ova in 1993. Mean annual fecundity based on estimates derived from the time-calibrated method were 1,292,544 ova for 1991 and ranged from 424,560 to 884,500 ova in 1993.

Maximum likelihood estimates were calculated for total length and for weight (Table 5). Estimates indicated that females reached first maturity at 200mm TL. Fifty-percent of females were mature by 229mm. All females larger than 509mm were mature. Fifty-percent of females were mature by 81g with all females mature above 1167g mature. Due to the lack of samples during the spawning season, maximum likelihood estimates could not be calculated for males. Sex ratios were calculated by sample source (Table 6) and by month of the year (Table 7). Females were more abundant than males in every identifiable sample source category other than LOOP.
Table 4. Comparison of spawning frequency estimates for female southern flounder sampled during 1991-92 and 1993-94 spawning seasons using the postovulatory and time-calibrated methods. Day-0 females (imminent spawners) are evidenced by the presence of late vitellogenic oocytes and day-1 (recent spawners) are those exhibiting POFs.

<table>
<thead>
<tr>
<th>Date</th>
<th>Mature Females</th>
<th>Females with POF</th>
<th>SF</th>
<th>Day-0 Females</th>
<th>SF</th>
<th>Day-1 Females</th>
<th>SF</th>
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<tr>
<td>12-12-91</td>
<td>17</td>
<td>6</td>
<td>2.9</td>
<td>6</td>
<td>6</td>
<td>2.9</td>
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<tr>
<td>12-13-91</td>
<td>19</td>
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<td>4.8</td>
<td>9</td>
<td>4</td>
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<td>12-17-93</td>
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<td>5.3</td>
<td>15</td>
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<td>12.5</td>
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<td>1</td>
<td>6.3</td>
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<tr>
<td>1-28-94</td>
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<td>1</td>
<td>8</td>
<td>4</td>
<td>1</td>
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</table>
Table 5. Maximum likelihood estimates calculated for female southern flounder sampled during 1987-1998 spawning seasons. Fifty-percent and one hundred percent maturity schedules were calculated. Estimates were calculated for total length and total weight.

<table>
<thead>
<tr>
<th></th>
<th>50% Maturity</th>
<th>100% Maturity</th>
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<tbody>
<tr>
<td>Total length</td>
<td>229mm</td>
<td>509mm</td>
</tr>
<tr>
<td>Total body weight</td>
<td>81g</td>
<td>1167g</td>
</tr>
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Table 6. Sex ratios of southern flounder sampled from 1987 to 1998 by month of the year. Samples taken in fishing tournaments were not included because of possible bias due to fishing location.

<table>
<thead>
<tr>
<th>Month</th>
<th>Females</th>
<th>Males</th>
<th>F/M Ratio</th>
</tr>
</thead>
<tbody>
<tr>
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<td>59</td>
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<td>14.8:1</td>
</tr>
<tr>
<td>Feb.</td>
<td>36</td>
<td>12</td>
<td>3:1</td>
</tr>
<tr>
<td>Mar.</td>
<td>31</td>
<td>21</td>
<td>1.5:1</td>
</tr>
<tr>
<td>Apr.</td>
<td>22</td>
<td>4</td>
<td>5.5:1</td>
</tr>
<tr>
<td>May</td>
<td>16</td>
<td>3</td>
<td>5.3:1</td>
</tr>
<tr>
<td>June</td>
<td>0</td>
<td>4</td>
<td>0:4</td>
</tr>
<tr>
<td>July</td>
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<td>Aug.</td>
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<td>Nov.</td>
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</tr>
<tr>
<td>Dec.</td>
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</tr>
<tr>
<td>Sample Source</td>
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<td>Male</td>
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<tr>
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<td>------</td>
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<td>Commercial</td>
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<td>Commercial-offshore</td>
<td>131</td>
<td>22</td>
<td>6:1</td>
</tr>
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<td>403</td>
<td>18</td>
<td>22.4:1</td>
</tr>
<tr>
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<td>126</td>
<td>5</td>
<td>25.2:1</td>
</tr>
<tr>
<td>LDWF</td>
<td>112</td>
<td>13</td>
<td>8.6:1</td>
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<td>LOOP trawls</td>
<td>14</td>
<td>24</td>
<td>0.58:1</td>
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<td>19</td>
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samples. Females outnumbered males by at least 12:1 for the months of July through January with the exception of October with a female to male ratio of 4.6:1. However, the number of males caught during the winter and spring are were not quite as low with female to male ratios of 3:1 in February, 1.5:1 in March, 5.5:1 in April, and 5.3:1 in May.
Discussion

Meristic Data

The maximum size of female southern flounder collected in this study was 764 mm total length. This fish was taken by rod and reel off the mouth of the Mississippi River on June 11, 1998 weighing 5953 g becoming the current state record for southern flounder. The maximum weight ever recorded for southern flounder is 9330 g. This fish was caught on Dec. 23, 1983 in Nassau Sound, in northeastern Florida.

The hypothesis that southern flounder display sexual dimorphism in age and growth is supported by length frequency distributions for males and females. Females had a distribution mode of 390 mm and reached up to 764 mm TL while males had a mode of only 280 mm and reached a maximum size of 414 mm. Shepard (1986) reported similar modal lengths with female mode at 358 mm and a male mode of 247 mm. Wenner et al. (1990) did not report modal lengths by sex but stated that forty-four percent of aged females were greater than 300 mm and few aged males were above 300 mm. The SEAMAP distribution had the same mode as males in this study at 280 mm while LOOP data had a mode of 240 mm. The similarities in distribution modes of SEAMAP, LOOP, and males in this study raise the possibility that males are more abundant in offshore samples collected by SEAMAP and LOOP.

The length-weight regression of log_{10} transformed data indicated the slope was significantly different from 3.0 (p = 0.0001) indicating growth is allometric; weight of the fish increases in relation to its size as length increases. Length-weight regressions on southern flounder produced slopes of 3.14 in South Carolina, 3.09 in Georgia, 3.10 in Florida, and 3.13 in Texas. These slopes were not tested to see if they were significantly different then 3 so it is unclear if there is significant allometric growth in
southern flounder from different regions. The higher slope suggests Louisiana southern flounder are more robust than those in previous studies.

Although both right and left otoliths may be used for age estimation, they display asymmetry in relation to the position of the core. Because the southern flounder lies on one side, the sagittae are positioned dorso-ventrally. The otolith on the left or “top” side of the southern flounder is asymmetric with the position of the core posterior to the center. This asymmetry is evident by the time the flounder reaches 68mm, the smallest specimen in the analysis. This is evidenced by the position of the core in otoliths of a reversed southern flounder. Southern flounder have sinistral eye symmetry where the right eye migrates to the left or “top” side at metamorphosis. The fish lies on its right side. Symmetry reversal is the change in directionality of eye migration (Policansky 1982) and is relatively common for some flatfishes in temperate waters (Cameron et al. 1992, Gudger 1935). This reversed flounder has dextral eye symmetry where the left eye migrated to the right side and the fish lies on its left side. This reversal is also evident in the otoliths. The position of the core in its right or “top” otolith is posterior to the center of the otolith and had a similar core index value as the left otoliths of normal southern flounder. The left or “bottom” otolith in the reversed southern flounder is symmetric.

Another Paralichthid with asymmetrical otoliths is the summer flounder (Paralichthys dentatus). Smith and Daiber (1977) reported a pattern of asymmetry in the otoliths but stated that the position of the core in the right otolith was asymmetric. Haas and Recksiek (1995) reported that the left sagitta, the otolith on the “bottom” side of the fish was more symmetric than the right in the winter flounder Pseudopleuronectes americanus. Hovenkamp and Witte (1991) stated that the core of Pleuronectes platessa otoliths was often located asymmetrically but they did not state if this was unique to the right or left otolith. Otolith asymmetry is variable between
species with no clear determination of the side in which the asymmetric otolith will be located. This along with the significant difference in right and left otolith weight warrants the consistent use of the right or left sagitta when dealing with any type of otolith measurements to reduce the chances of variation. Additional research on left and right-handed flatfish may provide insight on the question of what factors might determine asymmetry in otoliths.

**Age and Growth**

Marginal increment analysis and plot of edge condition indicate that one opaque zone is deposited on the otolith between the months of January and May and that annuli on sectioned otoliths may be utilized for accurate age estimation (Barger 1985). A peak of fifty-six percent of individuals with an opaque zone at the growing edge of the otolith is consistent with that of Beckman and Wilson (1995). In a review of 49 studies on north latitude temperate populations using sectioned otoliths, Beckman and Wilson (1995) reported a mean percentage of 65% of individuals with an opaque zone at the growing edge of the otolith.

Analysis of sectioned otoliths of young of the year (YOY) and yearling southern flounder indicated they formed their first annulus as early as 200mm and up to 330mm TL. The first annulus began to form in January with all yearlings completing their first annulus by March. These findings are consistent with Powell (1982) who found first annulus formation in the summer flounder to take place between January and March. Stokes (1977) also reported lengths of up to 300mm by first annulus formation in southern flounder. Wenner et al. (1990) detected no delayed or “lost” first annulus. Therefore this variability in size at first annulus formation is most likely due to differential growth among individuals, which Fitzhugh et al. (1996) found accounted for the broad dispersion of lengths occurring in the first year.
Females live longer than males. Females reached a maximum age of just over eight years while males reached only four years. These findings are close to Wenner et al. (1990) who reported a maximum age of 7 years for females and 3 years for males. Although they employed the use of whole otoliths, their validation techniques of evaluating the edge condition of whole otoliths were similar to this study producing similar maximum age estimates for each sex. Music and Pafford’s (1984) maximum age of 6 years for a female came from a data set of only 198 fish. It is not unexpected that they found a lower maximum age considering that only 11 out of 1286 (0.009%) aged fish in our data set were 5 years or older. Nall (1977) reported a maximum female age of 10 years. However, this age estimate seems unlikely when taking into account his invalidated use of whole otoliths. Williams and Bedford (1974) stated that the main source of difficulty in using whole otoliths to age fish is the presence of secondary checks or rings that could be perceived as additional annuli and thus increase your age estimation. In all studies on southern flounder cited here, males have never been aged above three years.

Growth parameters from sex specific curves suggest rapid growth to age two for males and to age three for females. Maximum theoretical size was calculated at 326mm for males and 520mm for females. This study predicts more rapid growth and smaller maximum sizes for males and females then reported on southern flounder from South Carolina by Wenner et al. (1990). These parameters and the contrast of the Louisiana and world record suggest that Southern flounder occupying the cold temperate waters of the Atlantic appear to reach greater maximum sizes then those in the warm temperate waters of the Gulf of Mexico. These differences in sizes between the Atlantic and Gulf of Mexico populations suggest zoogeographic variation in population dynamics of southern flounder. Such variation has been suggested for red drum (Matlock 1987) and Atlantic croaker (White and Chittenden 1977).
These sex specific growth models included 22 unsexed young of the year fish ranging from 68mm to 214mm total length. Music and Pafford (1984) stated that sex could not be determined before 130mm for females or 232mm for males. Stokes (1977), however, reported that sexual differentiation was not possible for either sex before 170mm. Juvenile southern flounder have exhibited a capacity for high growth rate relative to other fishes (Fitzhugh 1993). The addition of unsexed juveniles into the growth models may account for the high growth coefficient (k).

Size is not a useful tool in estimating age of southern flounder. Great variability in length and weight exists in individuals of the same age classes as well as between sexes. For example, a 225mm male could range in age from 0.5 to three years while a 350mm female could range in age from one to four years. Age at length keys are not particularly useful in predicting age due to the asymptotic growth patterns in southern flounder. For many species otolith weight has been shown to be independent of body growth and continues to increase as the fish ages (Beamish 1979, Beckman et al. 1991, Reznick et al. 1989). Otolith weight was regressed against age to determine if otolith weight could be used to estimate age. Four regressions were run: right and left otolith weight by sex. Although both models are adequate for females, the regression of age against left otolith weight in males is a better estimator of age. If otolith weight is going to be utilized as an alternative to age southern flounder, consistent use of the left otolith is suggested, but annulus counts from sectioned otoliths remain the most accurate estimator of age.

Reproductive Biology

The length of the southern flounder spawning season appears consistent throughout the years investigated in this study. Southern flounder spawning season, indicated by the presence of hydrated oocytes and postovulatory follicles, lasts approximately sixty days beginning in December and lasting through January. This
period of late fall to winter has been found to be the time of year for southern flounder spawning in a number of additional studies (Henderson-Arzapalo et al. 1988, Shepard 1986, Stokes 1977, Wenner et al. 1990).

Ovarian histology indicates reproductive preparedness in females begins in late October when primary growth oocytes begin to enlarge with the development of cortical alveoli. Transformation to the vitellogenic stage continues with the appearance of yolk globules in the periphery of the cytoplasm. Oocytes continue to incorporate yolk protein and reach late vitellogenesis with yolk globules throughout the cytoplasm by the end of November. The presence of all stages of oocyte development throughout the months of December and January indicates that southern flounder are batch spawners; they will develop multiple groups of oocytes throughout the spawning season and as long as conditions are suitable. Late stage vitellogenic oocytes, hydrated oocytes, and postovulatory follicles were observed in December and January indicating that spawning occurs during these months. The decline in vitellogenic oocytes in February as well as the onset of atresia indicates cessation of spawning (Hunter and Macewicz 1985).

GSI data corresponded well with ovarian histology indicating a preparation for spawning with slight increases in monthly mean GSI values in October and sharp increases in November and December. GSI values began to drop in January followed by rapid declines in February and March indicating the end of the spawning season. This drop in GSI values for the month of January indicates a peak in spawning activity for that month. Shepard (1986) found GSI levels began to increase a bit earlier with slight increases in August and maximum GSI values by November. Shepard (1986) stated a decline in GSI values in December indicating a peak in spawning activity for that month although he was unable to acquire samples from January through April and was therefore unable to determine the extent of the spawning season for his study.
Batch fecundity estimates for this study ranged from 14,046 to 68,829 ova per batch, and mean batch fecundity estimates of 62,473 ova for 1991 and 44,225 ova for 1993. Our mean yearly batch fecundity estimates were significantly different from each other. The significant variation in batch fecundity for years as well as the lack of correlation between batch fecundity and total length, total weight, eviscerated body weight, gonad free body weight, or age is most likely attributable to the small number of females used to determine fecundity.

Southern flounder fecundity estimates from this study were greater than previously reported. Arnold et al. (1977) reported a total of 120,000 eggs from a study of six mature females from 12 separate photoperiod and temperature induced spawns. This translates to roughly 1,600 ova per female per spawn. Lasswell et al. (1978) used hormone–induced strip-spawning methods on three females to obtain an average of 6,250 ova per female per spawn and an annual fecundity of 31,250 ova. In both studies, the methods by which these estimates were obtained as well as the low number of females in each study may have resulted in low fecundity estimates.

Behavior of the fish may have been altered due to the research conditions in which the fish were under. While observing spawning behavior of southern flounder under induced temperature and photoperiod conditions, Henderson-Arzapalo et al. (1988) stated that “Attempts to observe egg releases were disruptive, and fish immediately burrowed into the sand substrate precluding observation of spawning fish.” Henderson-Arzapalo et al. (1988) also had low batch fecundity estimates ranging from 66 to 28,900 ova per batch. Although Henderson-Arzapalo et al. (1988) stated that batch fecundity was inherently small when compared to most cultured flatfish, White and Stickney (1973) stated that female flatfish in general often lay over 100 thousand ova per spawning season.
An Analysis of Variance on batch fecundity estimates indicated that southern flounder gonads are not homogeneous. Therefore, fecundity estimates were calculated as a mean of replicates from each of the six regions of the ovary. Batch fecundity estimates are actually estimates of the numbers of hydrated oocytes; therefore it is actually the number of hydrated oocytes that are heterogeneous throughout the ovary. Tissue samples taken for histology slides to assess oocyte development were randomly taken throughout both lobes of the ovary. The plot of monthly percent oocyte stages based on these samples shows no indication of heterogeneity of primary growth, cortical alveolar, or vitellogenic oocytes. Perhaps the different developmental stages of oocytes are homogeneous but hydrating vitellogenic oocytes are not. Since it does not appear that the posterior ovarian horn possesses a lumen, hydrated oocytes may migrate towards the ovary lumen at the anterior end of the lobe where the oviduct is located. The heterogeneity may also be due to the small amount of females available for the analysis. Additional work in the future in which more females are available may produce more accurate fecundity estimates as well as a clearer determination of homogeneity of southern flounder ovaries.

First maturity in females was found to be at 200mm total length based on the presence of vitellogenic oocytes through microscopic examination of prepared histological slides. Fifty-percent maturity was determined through PROBIT analysis at 229mm with all females above 509mm mature. Shepard (1986) stated that smallest female with spawning potential based on GSI values was at 243mm total length, but did not state what GSI value would constitute a fish with spawning potential. Wenner et al. (1990) determined first maturity at 320mm with all females above 380mm mature. They used macroscopic examination of ovaries and determined maturity as the presence of “many large, free flowing hydrated oocytes.” With the relatively small fecundity estimates reported, hydrated oocytes may be difficult to observe with the
human eye. Wenner et al. (1990) noted a wide size range of developing animals but reported a difference of only 60mm from first maturity to 100% maturity. Wenner et al. (1990) reported first maturity in males at 230mm with all above 310mm mature. The inability to acquire samples offshore prohibited me from determining maturity schedules for males. The difference between estimates in this study and others reported might be due to how maturity is defined which could affect the number of mature individuals in the calculations. The small number of individuals in the data set below 200mm could have also had an effect on the calculations and may have reduced maturity estimates.

Stokes (1977) reported that both males and females reached first maturity at two years of age. Wenner et al. (1990) stated that some males began maturation before the age of two and females began to mature before age three. Nall (1979) reported that the youngest maturing fish was six years. His inflated estimate is surely due to his use of whole otoliths for age estimation. A small number of females under the age of two prevented accurate estimation of maturity schedules by age. However, of females sampled during the spawning season, 9 out of 11 one-year old fish and 123 out of 128 two-year old fish were found to be mature. This suggests that females may reach 50% maturity shortly before their first birthday. All females were found to be mature by the age of three with the exception of one three year old (373mm, 567g) and one four year old (379mm, 936g). A group of SEAMAP samples obtained in November 1998 contained five males approaching their first birth date. Two individuals determined these males to be mature through histological examination of the testis. This lower estimate of maturity for males seems a more logical life history strategy. If males do not reach maturity until age two as suggested by Stokes (1977) and Wenner et al. (1990) then nearly all males will have only one spawning season in which to spawn and ensure the continuation of their genetic lineage.
Southern flounder spawn in the offshore waters of the Gulf of Mexico with male migration offshore proceeding that of females. Stokes (1977) reported that males begin to migrate offshore in early October and that males were not present in samples after 25th of November. Although males in this study were collected throughout the spawning season, the number taken inshore was greatest in October with a low female to male ratio of 4.6:1 indicating an early movement of males offshore. When examining sex ratios by source, LOOP trawls taken offshore produce a ratio favoring males 0.58:1. The ratio of offshore commercial samples favors females but is relatively low in comparison to other sample source ratios which could indicate increased numbers of males offshore as well. These ratios suggest a higher concentration of males in offshore waters.

Sex ratios by month suggest that although a small number of females begin to migrate offshore in October, the majority do not leave the estuaries until November. This conclusion is supported by the increase in female to male ratios for the months of November through January as well as the number of females sampled by hoop net and pound net in Barataria Pass during the months of November and December 1997. Females began to show up in both net types as they were leaving Barataria Bay in the beginning of November. Females continued to show up through mid December. Males were essentially absent in the samples after mid November with the exception of one male taken by hoop net in the first week of December. All male samples from the month of January were taken from offshore.

Data from this study suggest a unique life history strategy for southern flounder. Southern flounder spawn in offshore waters in late fall to winter. Juvenile southern flounder then move into estuarine nursery grounds from January through March. These juveniles remain in the nursery until they are reproductively mature and are able to spawn. Males begin to move offshore to spawn before females in early fall. Female
movement offshore begins in late fall and continues through December. Spawning occurs for approximately 60 days in the months of December and January after which females begin to return to inshore waters. Sex ratios suggest that mature males do not return inshore as females do but remain in offshore waters. A similar pattern was observed in southern flounder from Texas waters where tag returns indicated the probability that older males did not return to the bays after emigration but remained in the Gulf for the duration of their lives (Stokes 1977).

There are numerous research needs of southern flounder that should be addressed. Because southern flounder depend on offshore waters as well as the estuaries throughout their life cycle, research should be undertaken to include samples from both locations to give a complete picture of its life history. The compilation of a data set including fish from all size and age classes would provide more accurate maturity schedules which could be of use in determination of size restrictions, although their utility may be questionable due to the great variability in size at maturity in this species. In addition, a greater number of offshore samples during the spawning season would certainly lend to more accurate fecundity estimates as well as provide a clearer pattern of male and female movement in and offshore.
Conclusions

1. Total length frequency distributions for male and female southern flounder were significantly different with male distribution mode at 280mm and female distribution mode at 390mm.

2. Male body weight ranged from 19g to 936g and females ranged from 61g to 5953g.

3. The left sagittal otolith is asymmetric in relation to the position of the core posterior to the center. Weight is also significantly different between right and left otoliths.

4. Marginal increment analysis and edge condition plot indicate that one opaque zone or annulus is deposited on southern flounder otoliths between the months of January and May and that annuli on sectioned otoliths may be utilized for accurate age estimation.

5. Length frequency distributions of young of the year and yearling southern flounder indicate that they form their first annulus between 200mm and 300mm total length.

6. Females live longer then males reaching a maximum age of 8.5 years while males reached a maximum age of only 4 years.

7. Sex specific growth models are necessary for southern flounder. Growth parameters suggest rapid growth to age two for males and to age three for females with males exhibiting a higher growth rate and smaller maximum size then females.

8. Left otolith weight may be used as an alternative to age southern flounder although annulus counts from sectioned otoliths remain the most accurate estimator of age.

9. Southern flounder spawning season, indicated by the presence of hydrated oocytes and postovulatory follicles, lasts approximately sixty days beginning in December and lasting through January.

10. Mean batch fecundity estimates were determined for 8 females (4 in 1991 and 4 in 1993) and found to be significantly different between years. Mean batch fecundity by year was 62,473 in 1991 and 44,225 in 1993.

11. Annual fecundity based on spawning frequencies derived from the postovulatory follicle method ranged from 787,474 to 1,292,544 ova in 1991 and from 212,280 to 504,467 ova in 1993. Mean annual fecundity based on estimates derived from the time-calibrated method were 1,292,544 ova for 1991 and ranged from 424,560 to 884,500 ova in 1993.
12. Females reached first maturity at 200mm total length. Fifty-percent of females were mature by 229mm with all females mature above 509mm. Fifty-percent of females were mature by 81g with all females mature above 1167g total weight.

13. Sex ratios suggest a higher concentration of male southern flounder in offshore waters then in the estuaries.
Literature Cited


Andrew James Fischer was born December 8, 1970 in Hamilton, Ohio. Upon graduation from Stephen T. Badin High School, he decided to pursue an undergraduate degree in Zoology at Miami University in Oxford, Ohio. He transferred to Louisiana State University in 1992 and took a student worker position with Dr. Bruce Thompson of the Coastal Fisheries Institute. His exposure to and interest in fisheries research led to an undergraduate research grant (UROP) funded by Sea Grant to study southern flounder otoliths. He received his Bachelor of Science in Zoology from Louisiana State University in December 1995. After graduation, he continued to work as a Research Associate with Dr. Thompson on a study examining the migration of zebra mussels along the Mississippi River. His interest in southern flounder life history led him to enroll in the graduate program at Louisiana State University in the Department of Oceanography and Coastal Sciences in June 1996.
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Major Field: Oceanography and Coastal Sciences

Title of Thesis: The Life History of Southern Flounder (Paralichthys lethostigma) in Louisiana Waters

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