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Gary R. Fitzhugh  
*National Marine Fisheries Service*

William A. Fable Jr.  
*National Marine Fisheries Service*

Wallace L. Trent  
*National Marine Fisheries Service*

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## Life History Parameters of Gulf Flounder (*Paralichthys albigutta*) From Northwest Florida

GARY R. FITZHUGH, WILLIAM A. FABLE, JR., AND WALLACE L. TRENT

Age, growth, natural and total mortality, a length–weight relationship, reproductive seasonality, sex ratio, maturity, and reproductive potential by size were estimated for gulf flounder, *Paralichthys albigutta*, from northwest Florida. The study used a fishery-independent approach during three annual migratory spawning seasons to sample gulf flounder offshore (spearing by divers) and inshore (multipanel trammel nets). We found gulf flounder to be slightly smaller at  $L_{\infty}$  than other paralichthids (using either von Bertalanffy or damped growth functions), but gulf flounder obtained larger sizes and older ages than previously thought for this species [females to 575 mm total length (TL) and age 7, males to 373 mm TL and age 11], probably due to offshore sampling targeting more of the adult component of the stock. Given the older age structure than previously noted for this species, gulf flounder maturity and mortality estimates were similar to values reported for other U.S. paralichthids. Gulf flounder exhibited fall–winter gonad development with all evidence pointing to spawning occurring offshore. We estimated batch fecundity and spawning frequency, but it was apparent that there was a seasonal effect for both of these parameters, with increased oocyte density and nearly daily spawning occurring by late October to November, the peak period of development, also reflected in the gonadosomatic index.

Gulf flounder, *Paralichthys albigutta*, ranges from Cape Lookout, NC to Laguna Madre, TX generally in depths less than 91 m (Ginsburg, 1952; Simmons, 1957; Guthertz, 1967). In contrast to another common southeastern U.S. *Paralichthys* sp., southern flounder (*Paralichthys lethostigma*), the gulf flounder has an affinity for hard or sandy bottoms and higher salinities during early life history. This habitat preference is shared with summer flounder (*Paralichthys dentatus*); however, gulf flounder tends to replace summer flounder at lower latitudes (Ginsburg, 1952).

Gulf flounder, along with southern flounder and summer flounder, is targeted commercially and recreationally in the southeastern United States but is considered common only along the Florida west coast where it dominates the paralichthid catch and reaches its peak abundance (Topp and Hoff, 1972; Murphy et al., 1994). Florida landings of flounder in 2005 were 788,824 pounds, with landings historically ranging over 1 million pounds. Recreational harvest is the largest fisheries component, taking about 67% of the total landings in 2005 (Florida Fish and Wildlife Conservation Commission, 2006).

While recognized as a valued and targeted species, no distinct trends or fishery concerns have been noted for gulf flounder. Florida provided an initial assessment in 1994 (Murphy et al., 1994), with periodic updates in catch trends (see Florida Fish and Wildlife Conservation Commission, 2006). A Gulf of Mexico

regional flounder management plan was developed in 2000 (Gulf States Marine Fisheries Commission, 2000). Standardized commercial catch rates for mixed flounder from Florida's gulf coast have been steadily increasing between 1992 and 2005. During this period standardized recreational landings for gulf flounder have fluctuated but were overall deemed stable (Florida Fish and Wildlife Conservation Commission, 2006). However, formal assessment and the ability to track trends have been hindered by the lack of species identification from the mixed flounder catch, so the status of gulf flounder should be viewed cautiously (Mike Murphy, pers. comm., Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL).

Life history and fisheries information for gulf flounder are sparse. Stokes (1977) reports on the age, growth, maturity, reproductive seasonality, diet, and distribution of gulf flounder from Texas estuarine waters. Topp and Hoff (1972) provide some information on seasonality and depth of spawning in the eastern Gulf of Mexico. Palko (1984) compares hard parts for aging gulf flounder, and Safrit and Schwartz (1988) provide the lengths and weights of 75 gulf flounder speared over a period of years from North Carolina waters. Murphy et al. (1994) provide information on growth and meristics for 67 gulf flounder sampled from Florida waters.

Our objective was to expand the life history information available for *P. albigutta* to increase

the chances for successful long-term management. Ours is the first study to target gulf flounder in the northeastern Gulf of Mexico and to sample the population in both offshore and inshore waters using a fishery-independent approach. Our particular region of study within northwest Florida may correspond to a zenith of abundance within the range for gulf flounder (see table 15 in Nelson and Monaco, 2000).

#### METHODS

*Sampling.*—Our collection methods and gear characteristics were previously reported for the samples analyzed herein (Fitzhugh et al., 2002). Briefly, we used multisized trammel nets in the lower St. Andrew Bay system as flounders were making fall movements from bay to offshore waters. Using scuba, we also speared flounders offshore by targeting their aggregations on natural and artificial reef habitat. Thus, our sampling took place each year between late Aug. and March (1996–1999; three annual migratory spawning seasons). Southern flounder was also commonly caught using the trammel nets, and we were able to readily distinguish gulf and southern flounder on the basis of published characteristics (Ginsburg, 1952; Gutherz 1967).

*Aging, growth, and mortality.*—Specimens were stored on ice in the laboratory until time of processing; usually within 24 hr of capture. Each fish was weighed to the nearest gram and total length measured to the nearest millimeter. Both sagittal otoliths were removed and stored dry. Sagittae were read whole, immersed in a solution of 95% ethanol, and viewed using reflected light against a black background. Annuli (opaque zones) were counted, and often both sagittae from an individual were examined. Our interpretation of opaque zones as an annulus is based on several aging studies of paralichthid flounders that used marginal increment analysis to validate annulus formation (Pattison and McAllister, 1990; Wenner et al., 1990; and Stunz et al., 2000). Because each sampling season occurred from fall through winter, well after the expected completion of opaque zones (complete by spring–early summer), annulus count was equivalent to annual age for individuals captured from Sep. through Dec. For those individuals captured after Jan. 1, we advanced the annual age on the basis of convention (Jearld, 1983). Some sagittae were sectioned to compare whole and sectioned otolith ages. We sectioned all otoliths with whole-age estimates equal to and greater than age 4. Our sectioning methods follow Cowan et al. (1995). We viewed sections with transmitted light

at  $\times 20$  magnification and made counts of annuli (opaque zones) similar to our procedure with whole otoliths.

We calculated average percentage error (APE) in aging for two readers following Beamish and Fournier (1981). Biological age (fractional age) was used in growth and fecundity functions and was calculated as the difference between the peak spawning date and the capture date; this fractional period added to or subtracted from the annual age. The von Bertalanffy growth parameters were calculated using the function SOLVER in Microsoft EXCEL (Haddon, 2001):

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

where  $L_t$  = length at time  $t$ ,  $L_\infty$  = asymptotic length,  $K$  = Brody growth coefficient, and  $t_0$  = theoretical age at length = 0. We used the damped growth equation (Porch et al., 2001) to model a pattern of growth common among some tropical and subtropical fishes where extremely rapid growth occurs during the transition from juvenile to young adult, followed by little growth as adults:

$$L_t = L_\infty \left[ 1 - e^{\beta - k_0(t-t_0)} \right]$$

$$\beta = [k_1(e^{-\lambda t} - e^{-\lambda t_0})] / \lambda$$

where  $L_\infty$ ,  $t$ , and  $t_0$  are as above,  $\lambda$  = a damping coefficient, and  $k_0$  and  $k_1$  = growth rate coefficients.

We estimated the instantaneous rate of natural mortality ( $M$ ) from the following functions (1)  $\log M = -0.0066 - 0.279 (\log L_\infty) + 0.6543 (\log k) + 0.4634 (\log T)$  where  $L_\infty$  and  $k$  are von Bertalanffy growth parameters, and  $T$  = the mean annual bottom water temperature in our region (Pauly, 1980) and (2)  $\ln M = 1.46 - 1.01 (\ln \text{maximum age})$  (Hoenig, 1983). Hoenig's method actually calculates  $Z$ , the total instantaneous mortality rate, but the original regression was based on lightly exploited stocks so an assumption is that Hoenig's longevity-based function is a good estimator of natural mortality. Our estimates of the instantaneous rate of total mortality ( $Z$ ) were derived on the basis of catch curves from gulf flounder collected offshore.  $Z$  is estimated from the negative slope of the right descending limb of the natural log-transformed catch curve (Haddon, 2001). We also calculated the sex-specific annual survival rates ( $S$ ) using the Robson and Chapman (1961) estimator and converted them to instantaneous mortality estimates ( $Z$ ; see MacNair et al., 2001).

TABLE 1. Macroscopic/histological characters of gonads for reproductive staging of *Paralichthys albigutta*. Maturity is defined as stage 3 and greater.

Stage	Macroscopic characters	Histological/microscopic characters
<b>Females</b>		
1.	Immature; sex can be distinguished.	Primary oocytes; large nucleus relative to area of cytoplasm.
2.	Ovary small, no vitellogenic oocytes detectable by eye.	Cortical alveolar stage; white yolk vesicles appear in most advanced oocyte stage.
3.	Early vitellogenesis; oocytes are visible to the naked eye through the ovarian tunic.	Vitellogenic oocytes are the most advanced stage, yolk vesicles and globules common; yolk vesicles appear red in sections.
4.	Late vitellogenesis; sexual products ripe but not extruded under light pressure.	Vitellogenic oocytes larger than about 400 $\mu\text{m}$ , vesicles and globules enlarged.
5.	Hydrated oocytes present, ova extruded under light pressure.	Hydration; nucleus migrates to animal pole, yolk coalescence, postovulatory follicles may be present.
6.	Spent; genital aperture inflamed, ovaries appear deflated.	Atretic material is common and greater than 50% of yolked oocytes are undergoing atresia.
<b>Males</b>		
1.	Immature; sex just distinguishable, testes translucent and small.	Mostly spermatogonia are present; other stages not readily distinguished.
2.	Developing; testes larger than stage 1, testes translucent to grayish red.	All stages of development present (spermatogonia, spermatocytes, spermatids), germinal epithelium is continuous.
3.	Developing; white opaque testes with blood capillaries detectable.	Tubules full of sperm, no sperm accumulation in deferent duct, germinal epithelium is discontinuous.
4.	Testes reddish white, capillaries prominent, no milt extruded under pressure.	Tubules full of sperm and sperm begins to accumulate in the deferent duct.
5.	Testes reddish white, milt extruded with light pressure.	Same
6.	Spent; testes appear deflated, testes red.	Spent, testes in regression, cells appear fused and form semicontinuous mass.

*Maturity and reproduction.*—Gonad weight, sex, and macroscopic stage were recorded to assess reproductive condition. Gonads from most flounder collected offshore during the spawning season were also subject to histological assessment to test our macroscopic stage identifications and to identify individuals with postovulatory follicles, which can be useful for spawning frequency determinations (following Hunter and Macewicz, 1985). We performed this extra effort for offshore fish because all our preliminary observations indicated that spawning, as evidenced by hydrated females, was occurring offshore. During the 1998–99 sample year, we randomly sampled the inshore flounder catch (every fifth flounder sampled) for histological assessment to compare with tissues of offshore flounders. Gonad tissue was dissected from the middle of either the left or right lobe and fixed in neutral buffered 10% formalin. Tissue sam-

ples were shipped to the School of Veterinary Medicine at Louisiana State University for processing into histological slides. Histological treatment included tissue dehydration, paraffin embedding, sectioning and staining with Gill's hematoxylin, and counterstaining with eosin (H&E sections). The macroscopic and histological stages we used (Table 1) are modified from Nikolsky (1963) and Garcia-Diaz et al. (1997). We also removed a few grams of ovarian tissue from each female with a visibly hydrated ovary, fixed the tissue sample in 10% formalin, and made counts of hydrated ova from subsamples of these tissues to generate batch fecundity estimates (Hunter et al., 1985). We documented seasonal reproductive development and estimated the date of peak spawning by using the gonadosomatic index (GSI), which is the ratio of gonad weight to somatic weight (total body weight minus gonad weight). GSI values were

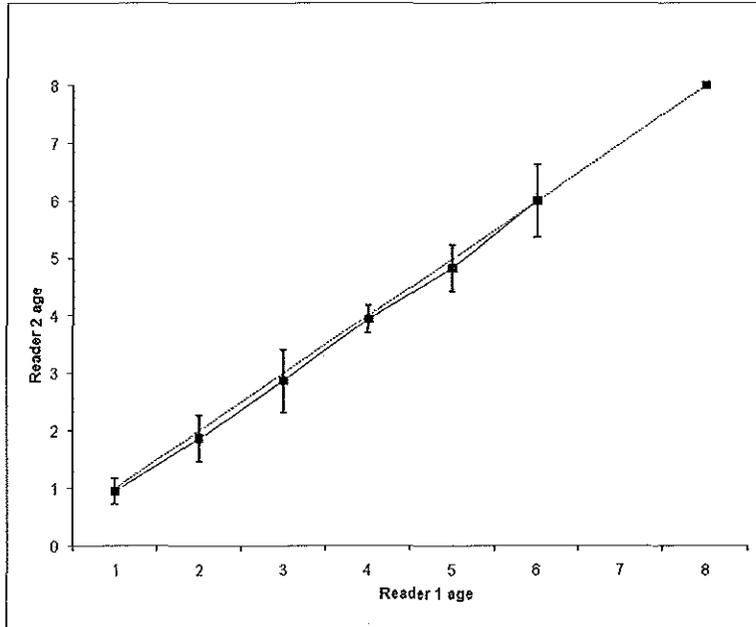


Fig. 1. Age bias plot for two age readers; expressed as mean and standard deviation of reader 2's annulus counts given reader 1's annulus counts. Dashed line represents 1:1 agreement.

tested for location differences (inshore vs offshore) by sex using the Mann-Whitney U-test.

All specimens at histological or macroscopic stage 3 or greater (Table 1) were designated mature. Specimens were assigned to 25-mm total length classes, and the proportion mature was related to the midpoint of each length class using logistic regression weighted by the numbers in each length class. The logistic model,

$$P_x = 1 / \left[ 1 + e^{-(a+bTL)} \right],$$

where  $P_x$  = proportion mature in each length class;  $a$  and  $b$  = fitted parameters; and length at 50% maturity,  $L_{0.5} = (-a/b)$ , was fitted to the data using maximum likelihood (logistic regression, XLSTAT version 7.5 analytical software).

## RESULTS

*Field sampling.*—Results from field sampling including locations, dates, and gear-specific length compositions are given in Fitzhugh et al. (2002). Briefly, 1,180 gulf flounder were sampled during three annual migratory spawning periods within St. Andrew Bay (fall–winter 1996, 1997, 1998–99). In addition, 274 gulf flounder were sampled by scuba divers at 15 offshore sites within 30 km of the bay entrance. From these collections, aggregated across years, flounder

were aged and fundamental life history parameters were estimated.

*Evaluation of aging.*—For comparisons of aging, otoliths from 1997–98 and 1998–99 samples including 836 flounder were independently aged by two of us (GRF and WAF), resulting in minimal reader bias and initial agreement on 90% of the annulus counts (Fig. 1). Within  $\pm 1$  yr, we agreed on 99.5% of our initial annulus counts and upon a review of count differences, we came to 100% agreement and ages were assigned. Our calculation of APE for the two readers was 4.7%.

Although processing time and cost increases for sectioned otoliths, only 5% of the flounders were estimated to be age 4 and greater on the basis of whole otoliths, so we sectioned each of the otoliths from the “older” fish. In addition, we randomly selected about 20 otoliths each from age 0, 1, 2, and 3 whole-age groups to use for a regression analysis of whole vs sectioned ages. In general, the linear fit of whole age to section age was very good, with an  $R^2$  value = 0.91, but the slope was greater than 1 (1.13) and indicates that after age 3 sectioned age tends to be greater than whole age with increasing error (Fig. 2). For example, our oldest flounder, a male that was initially estimated to be age 8 independently by both readers, was clearly

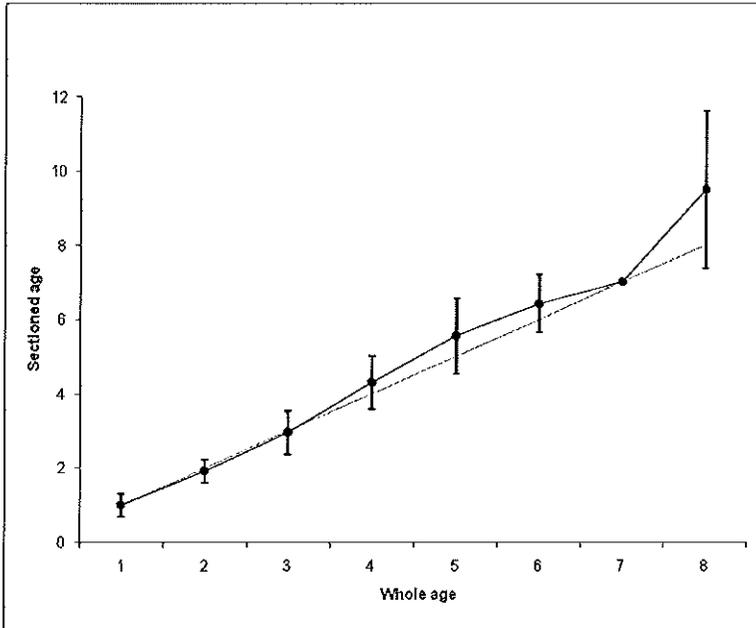


Fig. 2. Comparison of whole vs sectioned otolith ages. Dashed line represents 1:1 agreement.

observed to be older (estimated age 11) upon sectioning (Fig. 3).

*Age, growth, and length-weight relationships.*—Males and females exhibited obvious sexually dimorphic growth and size patterns, with females achieving larger sizes (Fig. 4). Estimated von Bertalanffy parameters for gulf flounder were:

females,  $L_{\infty} = 483.6$ ,  $K = 0.52$ ,  $t_0 = -0.97$  and males,  $L_{\infty} = 344.9$ ,  $K = 0.64$ ,  $t_0 = -1.46$ . For the damped growth equation for females, parameters were:  $L_{\infty} = 495.9$ ,  $k_0 = 0.42$ ,  $k_1 = 1.53$ ,  $t_0 = 0$ , and  $\lambda = 2.49$ . The damped equation parameters for males were:  $L_{\infty} = 348.5$ ,  $k_0 = 0.49$ ,  $k_1 = 2.8$ ,  $t_0 = 0$ , and  $\lambda = 2.41$  (Fig. 4). Despite sexually dimorphic growth, male and female size-weight patterns were similar for overlapping sizes, and a single length-weight relationship was developed for both sexes: total weight (g) =  $3 \times 10^{-6}$  [(total length) TL<sup>3.22</sup>] ( $R^2 = 0.96$ , range 208–575 mm TL; Fig. 5A). Older fish of both sexes were found offshore; the median biological age offshore was 2.8 yr for either males or females, and mean biological age inshore was 1.8 yr for either males or females (Fig. 6). Age ranges differed by sex and location; females ranged in age from 0 to 7 in both inshore and offshore locations, whereas males ranged from 0 to 3 yr inshore and 0 to 11 yr offshore.

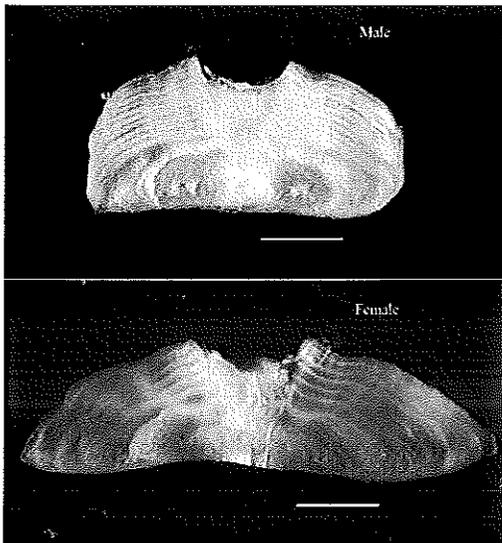


Fig. 3. Images from otolith cross-sections taken from male (353 mm TL, age 11) and female (500 mm TL, age 6) gulf flounder. The bar represents 1 mm.

*Mortality.*—For Pauly's (1980) method of estimating instantaneous rate of natural mortality ( $M$ ) we used the local mean annual bottom water temperature recorded offshore of Panama City Beach (21.6°C; Tolbert and Austin, 1959), and the previously reported von Bertalanffy parameters for the growth equation fit. For Hoenig's (1983) method of estimating  $M$ , we used the age of our oldest recorded male (11 yr) and female (7 yr). Our resulting estimates of  $M$  were (1) Pauly's method: 0.48 females and 0.6 males and

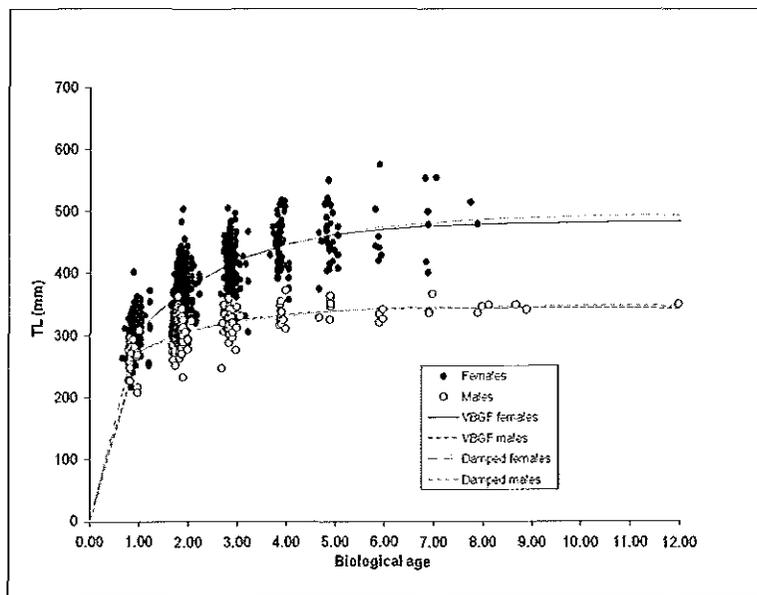


Fig. 4. Plots of observed size at biological age by sex with overlays of the von Bertalanffy growth function (VBGF) and damped growth function.

(2) Hoenig's method: 0.6 females and 0.38 males. We calculated the instantaneous rate of total mortality ( $Z$ ) for gulf flounder captured offshore by divers. The estimates for females were  $Z = 0.55$  females and  $Z = 0.42$  males for ages 1–7 (years combined; Fig. 7). Similar estimates were obtained using the Chapman–Robson approach;  $Z = 0.56$  females and  $Z = 0.47$  males. Our findings revealed that  $M$  is the largest component of  $Z$ , and that three (of four) approaches indicated a lower rate of mortality for males than females.

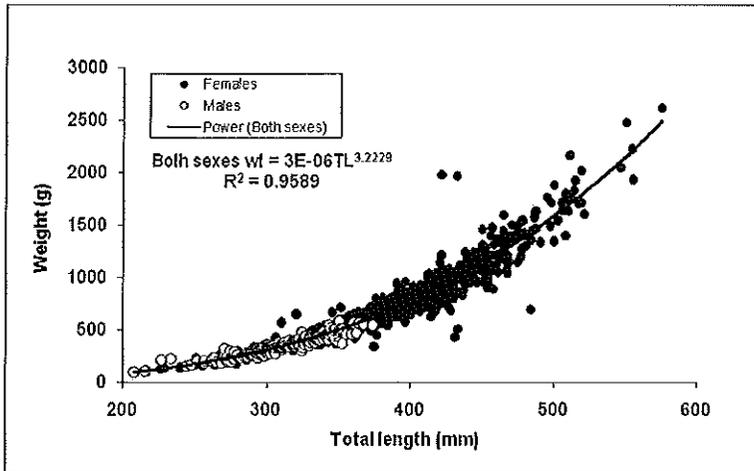
*Reproductive seasonality: GSI and histology of offshore flounder.*—The GSI shows that the general pattern of reproductive seasonality was synchronous for the two sexes (Fig. 8). Gonad weights increased dramatically between late Oct. and mid-Nov. On the basis of the temporal GSI pattern, it appeared that flounders were actively spawning in Nov. and Dec. and that spawning tapered off by Feb. However, sampling difficulties, problems locating flounders, and low sample sizes in Jan., Feb., and March prevented a clear understanding of cessation in spawning.

Results from histological staging corresponded well to the trends indicated by the GSI. Gulf flounder females with ovaries showing early development-stage oocytes—cortical alveolar stage—were apparent by Oct. By Nov. and Dec., hydration-stage ovaries dominated the collections of offshore females (Fig. 9). There was a

significant difference in the GSI for gulf flounders (male and female) between inshore and offshore collections as revealed by the Mann–Whitney U-test ( $P$  values for male and female GSIs  $< 0.0001$  for location differences). Values of GSI were much higher offshore, ranging to 10% for female and 4% for male and supported the observation that reproduction was only occurring offshore (Fig. 8). Further support for offshore spawning was indicated by the presence of hydrated females. Sometimes we noted an incidence of 100% hydration among offshore females. In contrast, only a single visibly hydrated female gulf flounder was noted from inshore trammel nets and none of the inshore females randomly sampled for histology were hydrated (Fig. 9).

*Sex ratio.*—Overall, the percentage of males increased in offshore collections from Sep. to Jan. while decreasing inshore during the same time period (Fig. 10). Offshore collections of gulf flounder had a sex ratio of 1:2.5 males to females for combined collections of Sep. and Oct., the period wherein annual sexual development begins. Inshore, a very similar sex ratio of 1:2.8 was estimated from trammel net catches. However, by Nov. and Dec. it was apparent that sex ratios were changing when spawning fish were detected. Males became much more frequent offshore, increasing in ratio to nearly 1 to 1 (1:1.3) and were not significantly different

A.



B.

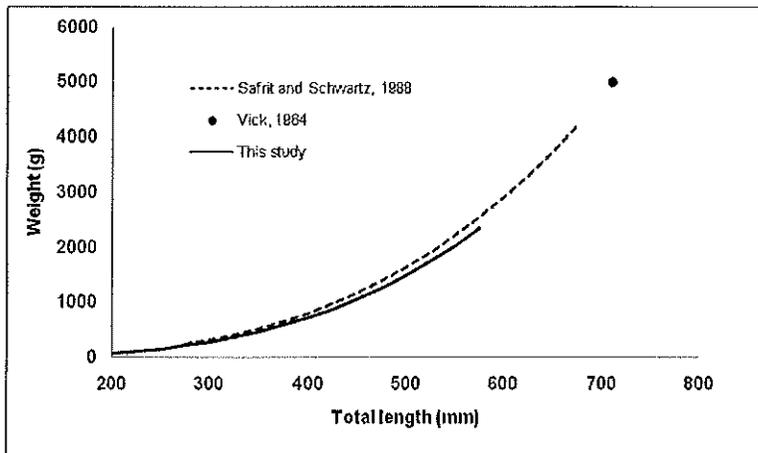


Fig. 5. (A) Length–weight regressions for observed data, and (B) comparison of length–weight functions (see Discussion).

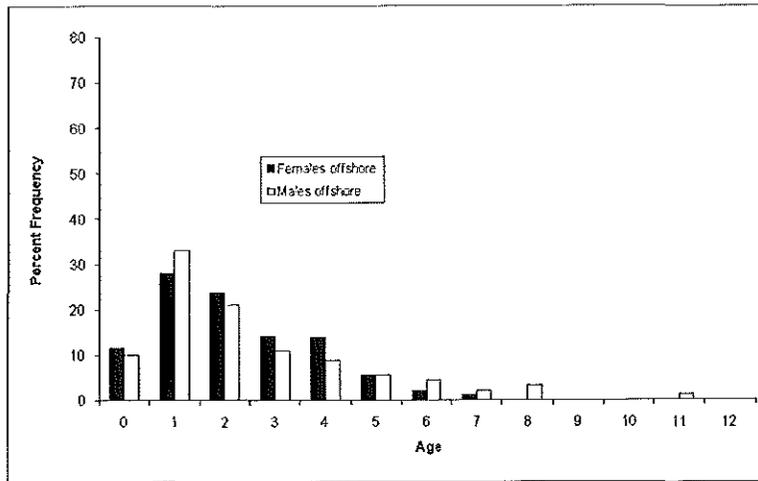
from expected chi-square 1:1 proportions ( $P = 0.21$  Nov.,  $P = 0.55$  Dec.). Although there were always more females encountered than males, Nov. and Dec. offshore collections were the only aggregations of the sample data that were not significantly different from a 1:1 ratio (Fig. 10).

*Assessment of maturity.*—On the basis of 75 males and 136 females staged both macroscopically and histologically during the peak reproductive period (Oct.–Jan.), there was 88% and 96% agreement between the two maturity methods for males and females respectively. These results indicate that females were more accurately assessed using macroscopic means than were males. For females, the presence of vitellogenic ova, the key trait of mature females

during the reproductive period, can be readily distinguished by macroscopic or histological observation. For maturity assignment of males, it is important to recognize stage 3: the rather imprecise macroscopic trait of white to reddish-white testes that is matched histologically by the accumulation of spermatozoa and discontinuous germinal epithelium.

Most maturity designations were based upon histology; we were able to add an additional 9 males and 28 females from offshore sampling that were assessed only by macroscopic staging, yielding a total sample size of 84 males and 164 females for fitting maturity functions. For both sexes, the logistic maturity relationships revealed an apparent asymptotic pattern (Fig. 11). Size at 50% maturity for female gulf flounders was 318 mm TL and for males was 263 mm TL. Thus

A.



B.

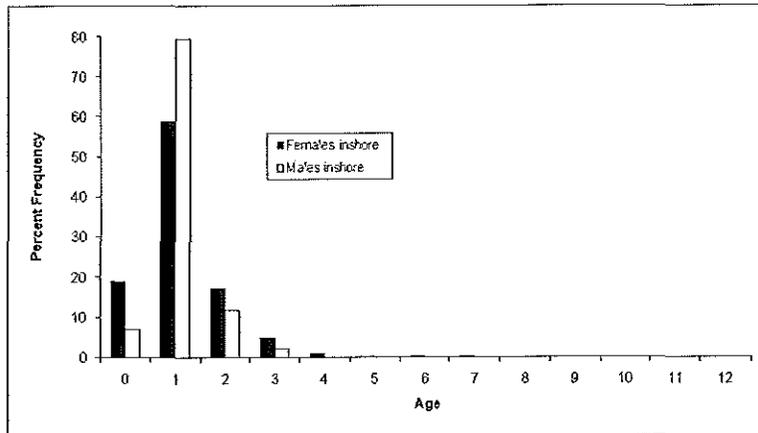


Fig. 6. Percentage frequency by age and sex for samples collected during the study from (A) offshore and (B) inshore.

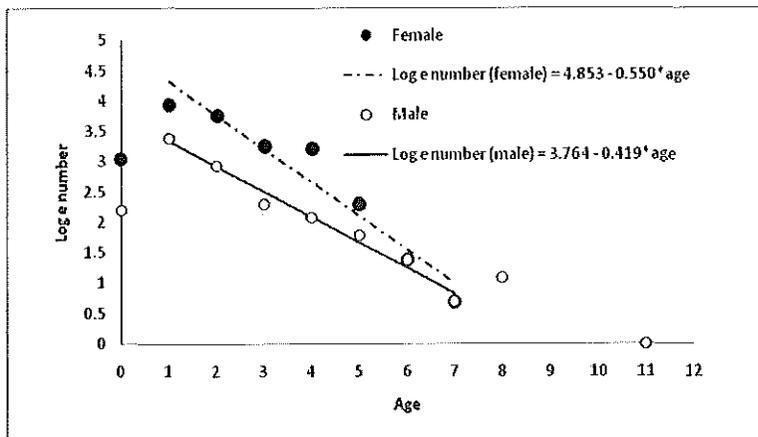


Fig. 7. Catch curves for males and females derived from offshore samples. Age-0 fish were not used in calculating the regression lines.

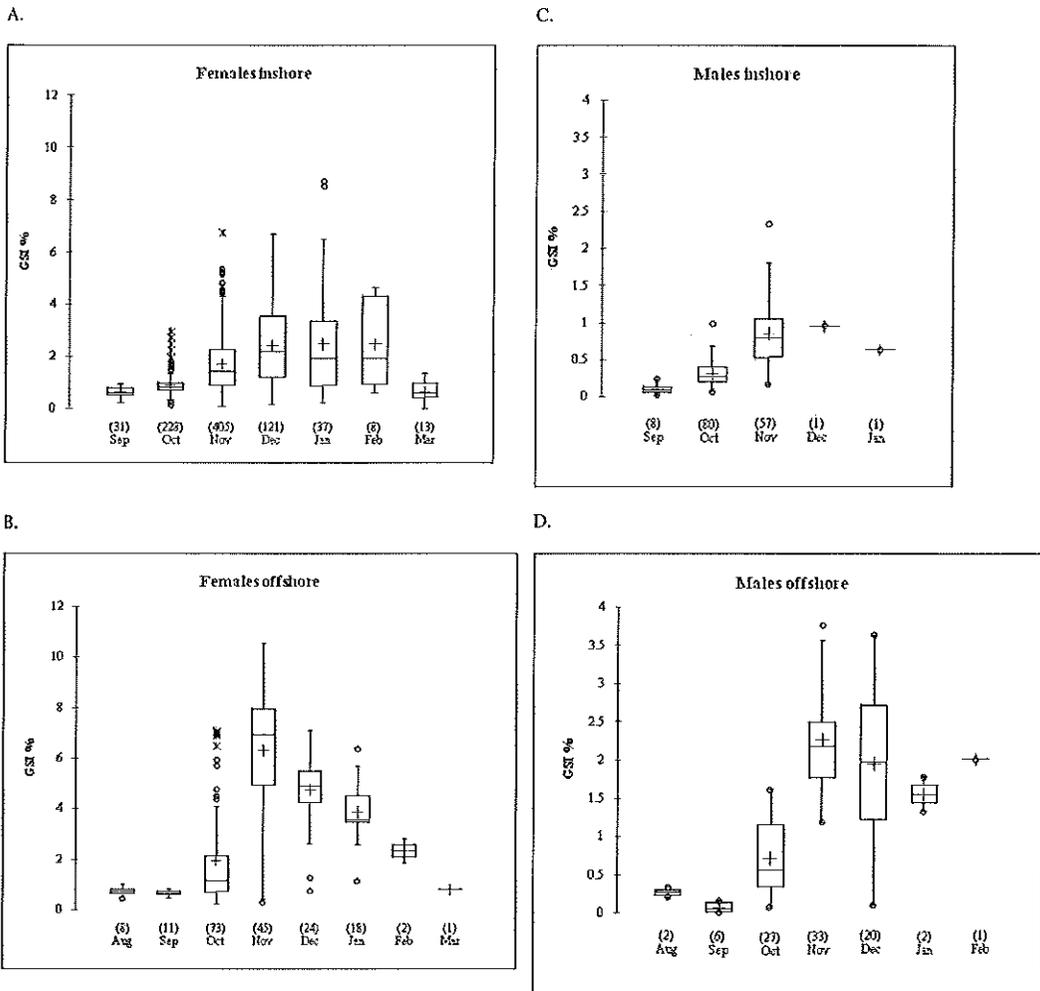


Fig. 8. Box plots of the monthly distribution of the gonadosomatic index (GSI %) for (A) females inshore, (B) females offshore, (C) males inshore, and (D) males offshore. Sample sizes are indicated in brackets; cross-hairs denote the mean.

a greater proportion of males are mature at a smaller size (most mature by 300–350 mm) in accordance with a sexually dimorphic growth pattern.

*Fecundity and spawning frequency.*—Spawning frequency estimates from the first 2 yr, 1996–97 and 1997–98, were similar and indicated that females were spawning about every day (range 1–1.32 d between spawns on average) by Oct. each year (Table 2). In 1998–99, fewer than 10 mature females were sampled, thus rendering an estimate inconclusive. But when spawning frequency was pooled across years, similar results were obtained using either the hydrated method (1.29 d) or the postovulatory follicle method (1.14 d).

Oocyte density (hydrated oocytes/g ovarian weight) was significantly different by month ( $P < 0.001$ ) and was greatest in Nov., mean (SD) = 1,296 (481), in contrast to Oct. 847 (558), Dec. 324 (392), and Jan. 38 (20). This peak in oocyte density in November corresponded with other measures of seasonal reproductive development (GSI, hydrated stage occurrence; Figs. 8 and 9). Because it is often of interest to gauge the relative differences in reproductive potential by female size or age at the point of peak development, we therefore restricted further fecundity analysis to Nov.-sampled females. The regression of batch fecundity and somatic weight provided the best-fit linear relationship ( $R^2 = 0.35$ ; Fig. 12A), compared with total length ( $R^2 = 0.28$ ; Fig. 12B) and biological age ( $R^2 = 0.07$ ).

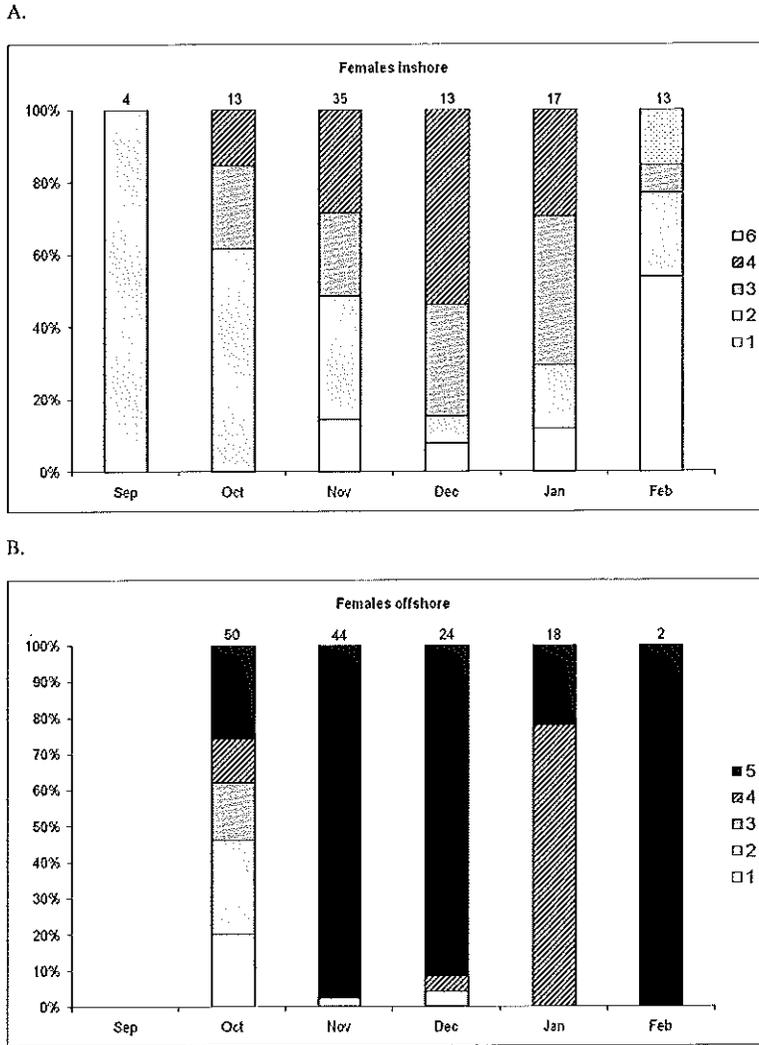


Fig. 9. Histological stage frequency by month for (A) females inshore and (B) females offshore. Stages 1 through 6 are defined in Table 1. Numbers above the bars indicate sample size.

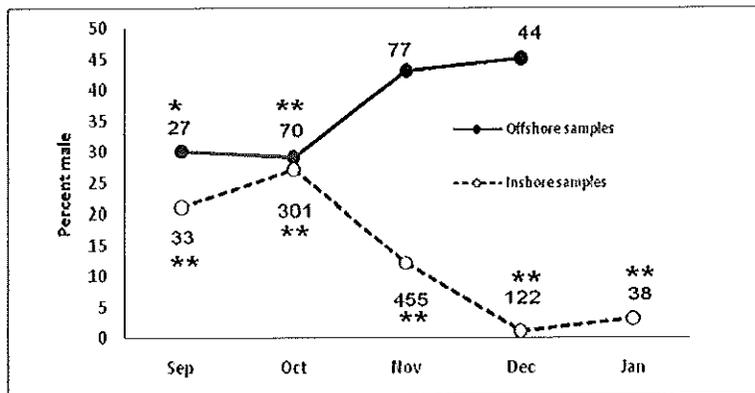
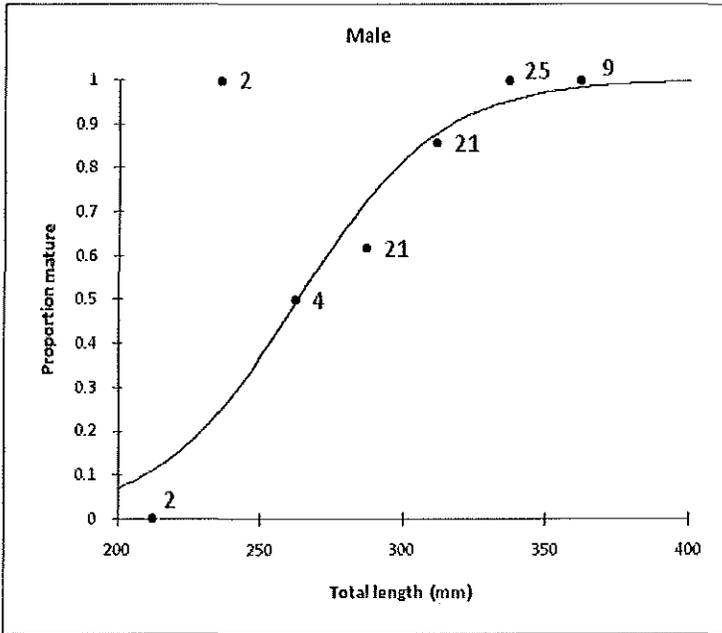


Fig. 10. Plot of percentage males in sample by month during the reproductive period for inshore and offshore samples. One offshore collection of 10 gulf flounder from late August (Aug. 28) was included in the September summation. \* =  $\chi^2$ ,  $P < 0.05$ , \*\* =  $\chi^2$ ,  $P < 0.01$ . N = sample size.

A.



B.

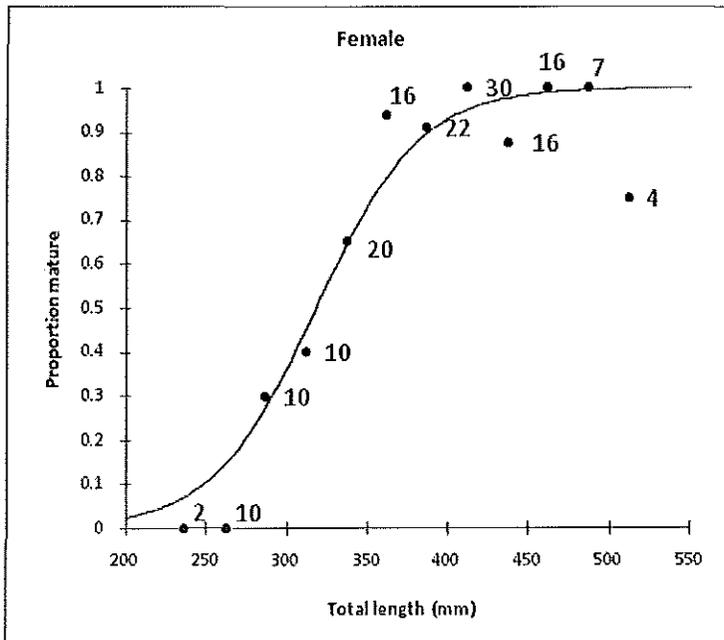


Fig. 11. Length-based maturity functions for (A) males: logistic curve parameters:  $a$ ,  $-10.685$ ;  $b$ ,  $0.041$ ; and (B) females: logistic curve parameters:  $a$ ,  $-9.962$ ;  $b$ ,  $0.031$ . One mature female  $>550$  mm not shown. N = sample sizes for each 25-mm size interval.

TABLE 2. Spawning frequency estimates on the basis of hydrated females (H) and females bearing postovulatory follicles (POF). Number of trips refers to offshore dive trips (after onset of spawning).

Year	# Trips	# Mature females	# POF bearing females	# H females	POF spawning interval (d)	H spawning interval (d)
1996–97	5	73	67	55	1.09	1.32
1997–98	2	24	24	24	1	1
1998–99	3	9	2	3	4.54	3
Total	10	106	93	82	1.14	1.29

We also measured ovary weight of advanced-stage Nov.-sampled females as a proxy for fecundity. The increased sample sizes afforded by using ovary weights resulted in improved equation fits and the equation with the greatest coefficient of determination was a power function of ovary weight and total length ( $R^2 = 0.63$ ; Fig. 13).

#### DISCUSSION

Our findings extend the limited life history information available for gulf flounder and indicate that longevity, growth, body sizes, and thus mortality estimates are more on par with congeneric species than previously understood. Also like congeneric species, gulf flounder is an important and targeted species, particularly in Florida waters. Given the potential that fishing may affect genetic/phenotypic selection, particularly for popular and targeted species with relatively short generation times (Law, 2000), this work may serve as a benchmark for measures of life history traits that likely are changing over time.

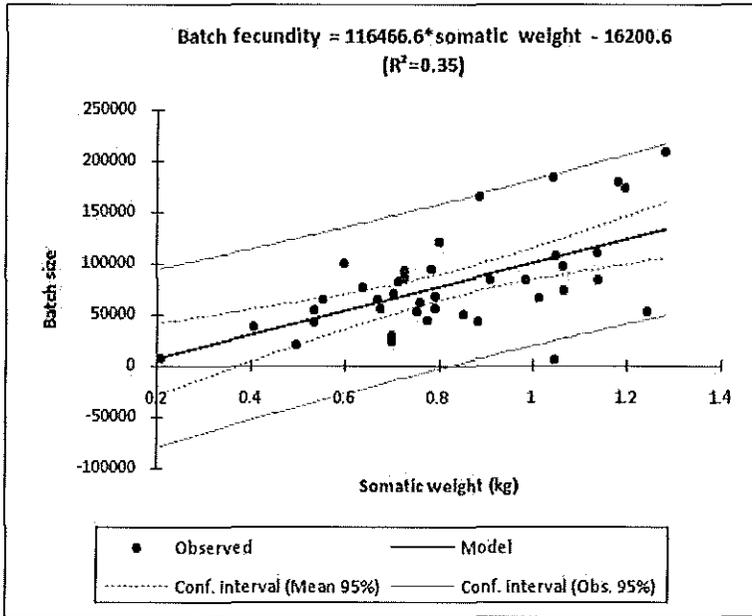
Our otolith age determination precision was good (APE = 4.7%) and meets a desired quality-control threshold (APE below 5%; Morison et al., 1998). This target APE can be difficult to achieve when only very young ages predominate (e.g. age 0 to age 2), as any differences between otolith readers will readily inflate the APE value. In preliminary age comparisons of flounder, disagreements in readings were obtained only for presumably old males. A general observation was that these male otoliths qualitatively appeared to be heavy for a given body size compared with females. Otoliths of older males (e.g. >4–5 yr) also were characterized by “stacking” of annuli and did not show the same degree of longitudinal growth in comparison with otoliths from faster-growing females. Thus, it may be feasible to reliably identify sex from random market sampling of gulf flounder otoliths, but sex-based differences between otoliths remains to be fully tested, especially among young fish. For routine aging, however, we believe that otolith sectioning

is only needed for fish that can be visibly seen to have more than three or four annuli and that are likely to be well in the minority from market or fishery-dependent samples (the adult portion of the stock). Refraining from having to section otoliths helps to minimize processing costs associated with aging fish.

Little information is available on growth for gulf flounder (see Stokes, 1977; Murphy et al. 1994), and ours is the first estimate of a growth function for gulf flounder. We noted that, similar to many tropical and subtropical species, growth is very rapid in the first year or two of life, followed by an asymptotic phase in which little growth in length is observed for the remainder of life. The von Bertalanffy growth function (VBGF) has problems fitting this size at age pattern and a common result is a negative estimated value for  $t_0$  (Craig, 1999; Porch et al., 2001), which we observed in our VBGF fits. Depending on the use of VBGF parameters, departures of  $t_0$  from an intercept of approximately zero can return biased estimates of growth and yield from a population model, particularly among the youngest ages. Thus we fit the damped growth function (Porch et al., 2001), which more realistically treated the early growth phase and provided estimates of  $t_0 = 0$ . Apart from differences between the functions with respect to  $t_0$ , estimates of  $L_\infty$  were very similar for the damped and VBGF functions and both approaches clearly illustrate differential growth by sex. Gulf flounder females obtain larger sizes ( $L_\infty = 496$  mm TL for the damped function) and grow faster than males ( $L_\infty = 349$  mm TL for the damped function). This is well known for paralichthid flounders (Matlock, 1991; Murphy et al., 1994; Stunz et al., 2000; MacNair et al., 2001; Fischer and Thompson 2004).

In the southeastern United States and Gulf of Mexico, more information on paralichthid growth is available for southern flounder. The comparisons reveal that gulf flounder  $L_\infty$  values are at the low end of the range of estimated  $L_\infty$  values for southern flounder, suggesting that gulf flounder are generally smaller sized. For

A.



B.

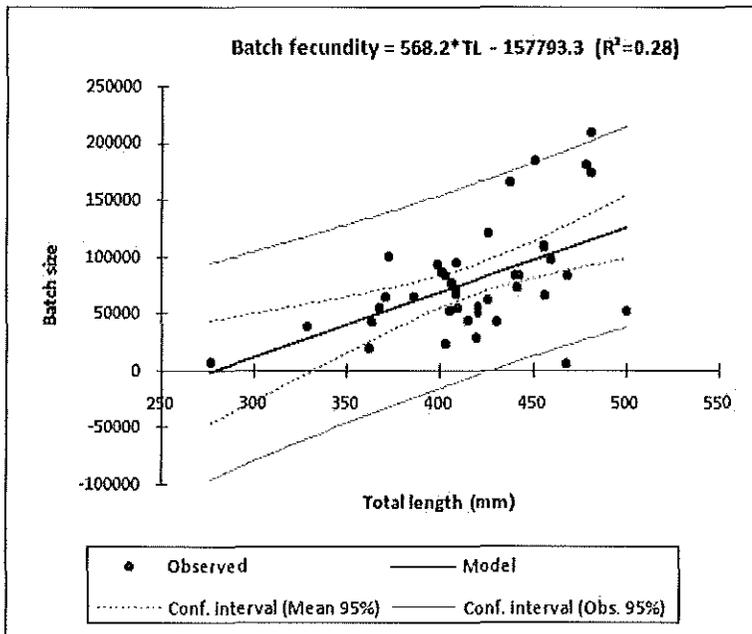


Fig. 12. Batch fecundity regressions by (A) somatic weight (kg) and (B) total length (mm).

instance, we estimated female gulf flounder  $L_{\infty}$  = 496 mm TL (damped function), whereas  $L_{\infty}$  values for southern flounder range from 483 mm to 759 mm TL (Wenner et al., 2000; Matlock, 1991; Stunz et al., 2000; Fischer and Thompson, 2004). Similarly, for male gulf

flounder our estimate of  $L_{\infty}$  = 349 mm TL (damped function) was at the low end of a  $L_{\infty}$  range of 332.5 to 518 mm TL for male southern flounder (Wenner et al., 2000; Stunz et al., 2000; Fischer and Thompson, 2004). Besides southern flounder, other U.S. paralichthids also reveal

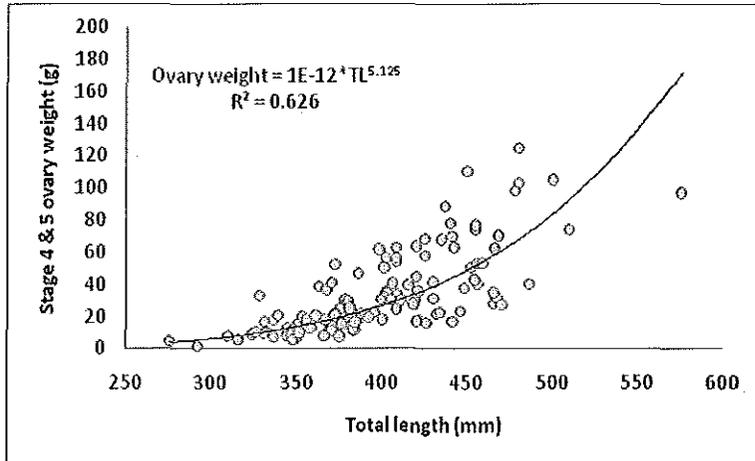


Fig. 13. Ovarian weight (g) by total length (mm), fit to power function as a proxy for fecundity. Only ovarian weights of females in advanced reproductive stages (4 and 5) are shown.

larger  $L_{\infty}$  values than gulf flounder (compare values for summer flounder, Virginia Marine Resources Commission 1999, and California halibut, *Paralichthys californicus*, MacNair et al., 2001).

Although generally smaller at  $L_{\infty}$  than other U.S. paralichthids, we found that gulf flounder obtained larger sizes and older ages than previously recorded for this species when sampling was focused on inshore waters (e.g., life history review by Gilbert 1986). Female gulf flounder ranged to 575 mm TL in our study, which was larger than reported by Stokes (1977; maximum = 420 mm TL). Vick (1964) reported a 710 mm TL gulf flounder from commercial catches landed at Panama City, and Safrit and Schwartz (1988) measured a gulf flounder female at 673 mm TL. Interestingly, Gilbert (1986) questioned Vick's report and wondered if the species identification may have been confused with a southern flounder, as at the time the largest recorded gulf flounder was noted to be 420 mm by Stokes. Safrit and Schwartz thought Vick's estimate a robust one because it seemed to fit on a length-weight regression line for gulf flounder from North Carolina; a regression that also matches our gulf flounder length-weight results (see Fig. 5b). However, we note that the length-weight regression for southern flounder from Louisiana (Fischer and Thompson, 2004) is also essentially the same as for gulf flounder; thus a length-weight relationship would not help support or refute species identification. We would like to believe Vick's measurement because it is likely both species were present in the commercial catches at Panama City in the 1960s and side by

side they can be readily distinguished even if the paralichthid flounders remain currently undifferentiated in routine port sampling. Thus, unlike Gilbert's (1986) conclusion, we think there is some possibility that gulf flounder can reach the size noted for southern flounder (*P. lethostigma*) and summer flounder (*P. dentatus*) (i.e., >700 mm TL). We also noted larger males than commonly reported. Our largest gulf flounder male equaled 373 mm TL, with males visually seen to asymptote at about 350 mm. Safrit and Schwartz (1988), who also sampled gulf flounder by diving offshore, reported a male as large as 426 mm TL. In a previous Texas study, the largest male reported was 290 mm TL (Stokes, 1977).

Similar to size trends, we found gulf flounder to be longer-lived than revealed in previous studies. Longevity was previously reported to be 2–3 yr for gulf flounder on the basis of a sample of 123 specimens of gulf flounder in Texas (Stokes, 1977). However, we captured males as old as age 11 and females as old as age 7. This raises the longevity of gulf flounder to similar ages recorded for other paralichthids (southern flounder; Wenner et al., 1990; Fischer and Thompson, 2004, and summer flounder; Wenner et al., 1990). Although our size ranges inshore and offshore were similar, inshore collections were dominated by ages 0, 1, and 2 and we sampled very few individuals as old as age 4 (males) and age 7 (females). Offshore, flounders were older, with most individuals between age 2 and age 8. Thus after gulf flounder migrate to offshore waters to spawn, older individuals may become increasingly resident offshore and the general idea of “back-and-

forth" annual spawning migrations between bay and ocean may not hold for oldest individuals. These data support previous suppositions as Stokes (1977) believed older gulf flounder may reside in deeper offshore waters.

In general, our estimates of natural mortality ( $M$ ) are similar to estimates reported for southern flounder considering that growth parameters and longevity are similar, particularly for females. Our estimates of  $M$  ranged from 0.48 to 0.6 for female gulf flounder using Hoenig and Pauly approaches. Using both these approaches for southern flounder, estimates for  $M$  ranged from 0.35 to 0.44, largely on the basis of data derived from females in Texas (Matlock, 1991) and from 0.47 to 0.59 for females in South Carolina (Wenner et al., 1990). The finding of older ages than previously reported for gulf flounder; especially for males, has important implications for estimates of mortality. Our estimates of  $M$  ranged from 0.38 to 0.6 for male gulf flounder. By comparison, Wenner et al. (1990), who sampled inshore and presumably younger components of southern flounder populations, had higher estimates of male natural mortality, ranging from 0.54 to 1.17 for two mortality estimation approaches.

Gulf flounder instantaneous total mortality ( $Z$ ) was quite lower than reported from other paralichthid studies. Our estimates of gulf flounder  $Z$  ranged from 0.47 (males) to 0.56 (females) using the Chapman–Robson approach and 0.42–0.55 using a catch curve regression. On the basis of tagging data to derive a fishing mortality estimate ( $F = 0.4$ ), Matlock (1991) concluded that  $Z$  must be at least 0.75 for southern flounder in Texas, and Wenner et al. (1990) estimated values of  $Z$  ranging from 1.22 to 1.37 in South Carolina. Viewing estimates of  $Z$  of Matlock and of Wenner et al. and given that our values for  $M$  overlap our estimates of  $Z$ , we believe it is quite possible that we underestimated  $Z$ . The Chapman–Robson and the catch-curve approaches, on the basis of pooled ages common in short-term investigations, assume constant age-specific survival and recruitment (steady state). Departures from the steady-state assumptions can result in biased estimates (Murphy, 1997), and examination of our offshore log-abundance results suggests that younger females (ages 1–4) were possibly subject to different levels of selection or recruitment than older females (ages 5–7). Although we can't eliminate the possibility of gear selection, we do not believe our gear (spearing by divers) was biased in favor of larger and older flounders, as we used a systematic sampling approach and commonly caught a similar-shaped but smaller species,

dusky flounder, *Syacium papillosum* (Fitzhugh et al., 2002). Our estimates of  $Z$  were derived from the offshore adult component of the stock and it is possible that confounding of emigration and mortality would be a particular problem if investigators relied on inshore sampling, which could result in inflated values of  $Z$  (the opposite of our concerns). Nevertheless, we found no evidence for the degree of offshore age truncation and high mortality rates (e.g. estimates of  $Z$  exceeding 2.0) that would implicate overfishing, as reported for summer flounder (Terceiro, 2002).

Our findings regarding reproductive seasonality point to a general pattern of fall–winter gonad development with a peak in November that appears synchronous for both sexes (on the basis of GSI and histology results). Further, all evidence pointed to offshore spawning. There was separation between the spawners and the nonspawning and immature components of the stock remaining inshore during the fall. This agrees with what is known or generally believed about gulf and southern flounders in the southeastern United States. (Topp and Hoff, 1972; Stokes, 1977; Wenner et al., 1990; Safrit and Schwartz, 1998; and Fischer, 1999). We also noted that this inshore–offshore separation of spawners and nonspawners coincided with a dynamic change in sex ratio. Although there were always more females than males in collections, it was apparent from changing sex ratios that males moved offshore in November and December to attend those females in spawning condition; the only periods in which sex ratio offshore was not significantly different from 1:1. However, we had a much more difficult time locating flounders in January–March and thus we don't have a clear understanding of either movements or the cessation in spawning that must have occurred in those coldest months.

Early in planning the study, we were concerned that the difficulty in assigning macroscopic stages would be problematic in estimating size/age at maturity. We were aware that reading histological tissue sections is often the best way to assess the reproductive state of an individual fish but is expensive in comparison with macroscopic assessments where the gonad is visually examined "in the round". However, the macroscopic approach seemed to work well for determination of gulf flounder maturity, especially for females where macroscopic and histological assessments agreed 96% of the time. Although we believe we can use our data to develop preliminary maturity schedules for males, in general, macroscopic staging for males was more difficult (88% agreement) as the macroscopic appearance of

the testis was not as well matched to histologically detected stages.

Because of similarities in size and longevity, it is not surprising that our maturity results (50% maturity at 263 mm TL males; 318 mm TL females) are very similar to reported values for summer flounder and reflect slightly smaller size at maturity than values reported for southern flounder. Morse (1981) found size at 50% maturity for summer flounder to be 240–270 mm TL for summer flounder males and 300–330 mm TL for summer flounder females. In a South Carolina study, male southern flounder were 47–56% mature between 280 and 300 mm TL and females were 40–57% mature between 340 and 370 mm TL (tables 2–6 in Wenner et al., 1990). Safrit and Schwartz (1998) found that southern flounder females were “running ripe” at +2 yr and at least 343 mm TL.

Similar to our findings of seasonal gonad development, there was an apparent seasonal effect for batch fecundity. A significantly greater hydrated oocyte density (oocytes per gram of ovarian tissue) was detected in November. Oocyte density was notably lower in October, December, and January. On the basis of peak levels in November, the best-fit relationship was detected between batch fecundity and weight, with an average batch fecundity of 79,892 (SD = 47,997). Estimates of spawning frequency (SF) also reflect the high reproductive activity in November, with spawning occurring nearly every day (SF = 1.14 postovulatory follicle method, SF = 1.29 incidence of hydrated females method). There is little information on fecundity of southeastern U.S. paralichthids, but Fischer (1999) estimated average batch fecundity of southern flounder at 62,473 and 44,225 in two different years ( $n = 4$  in each year). Hydrated oocyte density (and hence batch fecundity) in southern flounder was noted to be significantly different among regions of the ovary, necessitating multiple samples be used for the estimates (Fischer 1999). Fischer also noted lower spawning frequency estimates (basically spawning every 3 to 12 d depending on year and method).

Because of sample size constraints and difficulties estimating batch fecundity and SF, a proxy relationship for fecundity may be useful on the basis of the relationship between ovary weight of vitellogenic females and size or age. Not surprisingly, the increased sample sizes resulted in greater coefficients of determination than batch fecundity equation fits. However, use of gonad weight can be problematic because of the large variation in gonad weight that can

occur during a daily cycle of final oocyte maturation and hydration.

Principal remaining uncertainties about gulf flounder life history derive from incomplete knowledge of movements and offshore distributions, particularly during the winter months. This is true for other paralichthids as well (e.g., Fischer and Thompson, 2004). Improved spatial-temporal sampling would provide better knowledge of reproductive potential by size and age (e.g. SF) and routine aging could be used to monitor year-class and mortality trends. Although otolith growth and increment patterns were similar to related paralichthids, and inter-reader precision was good, validation of increment formation and studies of aging accuracy remain to be completed for gulf flounder. Certainly, gulf flounder is one of the highest ranked species in Florida in terms of species targeted on recreational trips (Florida Fish and Wildlife Conservation Commission, 2006). Improvements in routine sampling and reporting of statistics therefore seem warranted and efforts should be made to identify flounders by species in the landings.

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