Abstract—The red porgy (*Pagrus pagrus*) is an important component of the Gulf of Mexico reef-fish fishery, yet little information is available on this species's life history. We sampled 877 red porgy (194–489 mm TL) from the eastern Gulf of Mexico during 1995 and 1996 to assess their age structure, growth, mortality, spawning season, size and age at maturity, and batch fecundity. The average length of males was significantly greater than that of females, and the overall sex ratio (1:1.6 in favor of females) was significantly different from 1:1. Marginal-increment analysis indicated that one opaque ring is formed on red porgy otoliths during the late spring or early summer of each year. Ages ranged from 1 to 17 years, and most fish were 3 and 8 years old. Von Bertalanffy growth model parameters were L_∞=459 mm TL, K=0.111/yr, and t_0=–6.6 years for all aged fish. Growth rates in our study were lower than those in previous studies of Gulf of Mexico red porgy—perhaps the result of size-selective fishing. Pooled estimates of total instantaneous mortality were 0.62–0.87/yr based on recreational landings data and 0.54/yr based on commercial landings data. Red porgy are protogynous hermaphrodites. The length and age at which males composed 50% of the population was 345.5 mm TL and 5.3 years. Few immature females were observed in our collections (n=10). All females greater than 302 mm TL and age 4 were mature. Red porgy spawn during the winter and spring, and ripe females were caught from January to April.

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Age, growth, mortality, and reproduction of red porgy, *Pagrus pagrus*, from the eastern Gulf of Mexico

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The red porgy, *Pagrus pagrus*, occurs in the eastern Atlantic from the British Isles south to Angola and in the western Atlantic from New York to Argentina (Manooch and Hassler, 1978; Randall and Vergara, 1978). In the Gulf of Mexico (GOM), red porgy are usually found near hard-bottom areas off the west-central Florida coast and the Florida Middle Ground, and the Flower Garden Banks off Texas (Smith et al., 1975; Nelson, 1988). Studies of reef habitat along the southeastern United States indicate that red porgies are most common over inshore live-bottom habitats and over shelf-edge, rocky-rubble, and rock outcrop habitats (Grimes et al., 1982; Barans and Henry, 1984; Chester et al., 1984; Sedberry and Van Dolah, 1984).

Most red porgy caught in the GOM are landed in Florida. From 1986 to 1991, an average of 83.6% of the commercially caught and 76.7% of the recreationally caught red porgy were landed there (Goodyear and Thompson[1]). Red porgy are an important component of the Florida west coast commercial reef-fish fishery and rank thirteenth in total weight of reef fish landed in this area (Goodyear and Thompson[1]). In Florida commercial landings data, red porgy are not distinguished from other porgies. However, assuming that red porgies made up 50% of all porgies landed (Goodyear and Thompson[1]), the combined west coast 1995 and 1996 Florida landings of this species were estimated at 0.5 million pounds and had an estimated dockside value of $487,000 (Marine Fisheries Information System[2]). Over the same period, an estimated 242,000 red porgy were landed by anglers in Florida (Marine Recreational Fishery Statistics Survey[3]), 80% by charter boats or headboats (Goodyear and Thompson[1]).

Currently there are no regulations on red porgy harvest in the GOM. Fishery managers are concerned that the harvest of reef-fish species, such as red porgy, may increase if the fishery shifts effort from red snapper to these species because of increasing restrictions

[1] Goodyear, C. P., and N. B. Thompson. 1993. An evaluation of data on size and catch limits of red porgy in the Gulf of Mexico. Contribution report MIA-92/93-67. National Marine Fisheries Service, Southeast Fisheries Center, Miami Laboratory, Miami, FL.

[2] Marine Fisheries Information System. 1997. Unpubl. data. Florida Fish and Wildlife Conservation Commission, 100 Eighth Avenue SE, St. Petersburg, FL 33701-5095.

[3] Marine Recreational Fishery Statistics Survey (MRFSS). 1997. Unpubl. data. Fisheries Statistics Division, National Marine Fisheries Service, Department of Commerce, Silver Springs, MD 20910.

on the GOM red snapper fishery (Anonymous[4]). The red porgy fishery shifted from a predominately recreational fishery to a predominately commercial fishery between 1988 and 1991 (Goodyear and Thompson[1]). Owing to these changing dynamics within the red porgy fishery, the Reef Fish Stock Assessment Panel of the Gulf of Mexico Fishery Management Council recommended that age, growth, and reproduction studies be initiated for future stock assessments (Anonymous[4]). Red porgy are protogynous hermaphrodites and may be more susceptible to overfishing than gonochoristic reef-fish species such as snappers if size-selective fishing reduces the number of males available for spawning and thus limits the amount of sperm available for fertilization (Bannerot et al., 1987; Koenig et al., 1996).

Existing age and growth data for this species in the GOM are inadequate. Nelson (1988) used scales to age red porgy collected from the Flower Garden Banks off Texas in the early 1980s and reported a maximum age of 6 years. This value is much lower than maximum ages reported from other regions. Maximum ages, determined from scales, whole otoliths, and sectioned otoliths have ranged from 13 to 18 years (Manooch and Huntsman, 1977; Vassilopoulou and Papaconstantinou, 1992; Pajuelo and Lorenzo, 1996; Harris and McGovern, 1997; Vaughan[5]). Nelson (1988) suggested that the reason he did not observe fish as old as those observed by Manooch and Huntsman (15 years; 1977) was that fishing had removed older fish from the GOM. However, mortality rates in the South Atlantic Bight (SAB) are now greater than those reported by Nelson (1988) for the GOM, and SAB fish as old as age 18 have recently been reported by Vaughan.[5]

Little information is available on the reproductive biology of red porgy in the GOM. Female red porgy begin to transform into males at 221 mm fork length; however, the length at which females begin to mature in the GOM is unknown because the smallest female sampled by Nelson (1988) was 272 mm fork length and all females that he examined were mature. Spawning occurs in the winter and spring in the GOM, as has been reported for the SAB, Canary Islands, and Mediterranean Sea (Manooch, 1976; Nelson, 1988; Vassilopoulou and Papaconstantinou, 1992; Pajuelo and Lorenzo, 1996), although Ciechomski and Weiss (1973) reported, on the basis of larval collections, that red porgies may spawn in the Argentine Sea during the summer (December and January).

Basic life-history information is needed for use in assessments of red porgy stocks in the GOM. Although Nelson (1988) examined red porgy age, growth, and reproduction in the GOM; his study was limited by area (Flower Garden Banks off Texas), sample size (n=126), and aging structure (scales). Accurate ages are needed to develop growth models, develop age-length keys, and estimate total mortality. In addition, the annual periodicity of ring deposition in otoliths has not been validated for red porgy in the GOM. With the increasing reliance on estimates of spawning-potential ratios to describe a stock's condition, information on maturation schedules and sex ratios are also needed. The purpose of our study was to age eastern GOM red porgy accurately in order to develop age-length keys and growth models, to construct catch curves for deriving estimates of total mortality, and to describe the reproductive biology of this species.

Methods

Collections

Eastern GOM red porgy were sampled from headboat and commercial catches between October 1995 and September 1996. Total length (TL), fork length (FL), and standard length (SL) were measured to the nearest millimeter. Whole weight and gutted weight were measured to the nearest gram (g). The relationships between lengths, weights, and $\log_{10}$-transformed total lengths and weights were determined by least-squares regression (SAS Institute, Inc., 1985). Male and female regression lines of $\log_{10}$-transformed total lengths and weights were compared by using analysis of covariance (Snedecor and Cochran, 1971). Length-frequency distributions were compared by sample source and by sex by using the Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf, 1981). All length data are reported as total length unless stated otherwise.

Age, growth, and mortality

Thin sections of otoliths (sagittae) were used to determine the ages of fish. Otoliths were removed and stored dry in culture wells. The left otolith was serially sectioned across its anterior-posterior midpoint at 0.5-mm intervals by making a transverse cut with an Isomet diamond saw. Mounted sections were placed on a black field, illuminated with reflected light, and examined with a binocular dissecting microscope. The magnified images of otolith sections were transmitted by means of video camera to a video monitor. The number of opaque zones and the radial measurements from the core to the last opaque zone and to the edge of the otolith (otolith radius, Fig. 1) were recorded from the monitor by using a computer-driven, data-acquisition software package (Optimas Corp., 1996). Marginal increments were measured as the distance between the last opaque zone and the edge of the otolith.

To determine if zone counts were repeatable between investigators, two readers independently examined sectioned otoliths collected from fish collected during July and August 1996 (n=241). After the first reading, readers examined the sections together and compared zone counts to form a consensus about what constituted a zone. The two readers then re-examined the sectioned otoliths independently, and counts were compared again. Because agreement between

[4] Anonymous. 1993. Final report of the reef fish stock assessment panel. Gulf of Mexico Fishery Management Council, 3018 U.S. Highway 301 N, Suite 1000, Tampa, FL 33619-2266.

[5] Vaughan, D. S. 1999. Population characteristics of the red porgy *Pagrus pagrus* from the U.S. Southern Atlantic Coast. Report prepared for the South Atlantic Fishery Management Council. National Marine Fisheries Service, Beaufort Laboratory, 101 Pivers Island Road, Beaufort, NC 28516

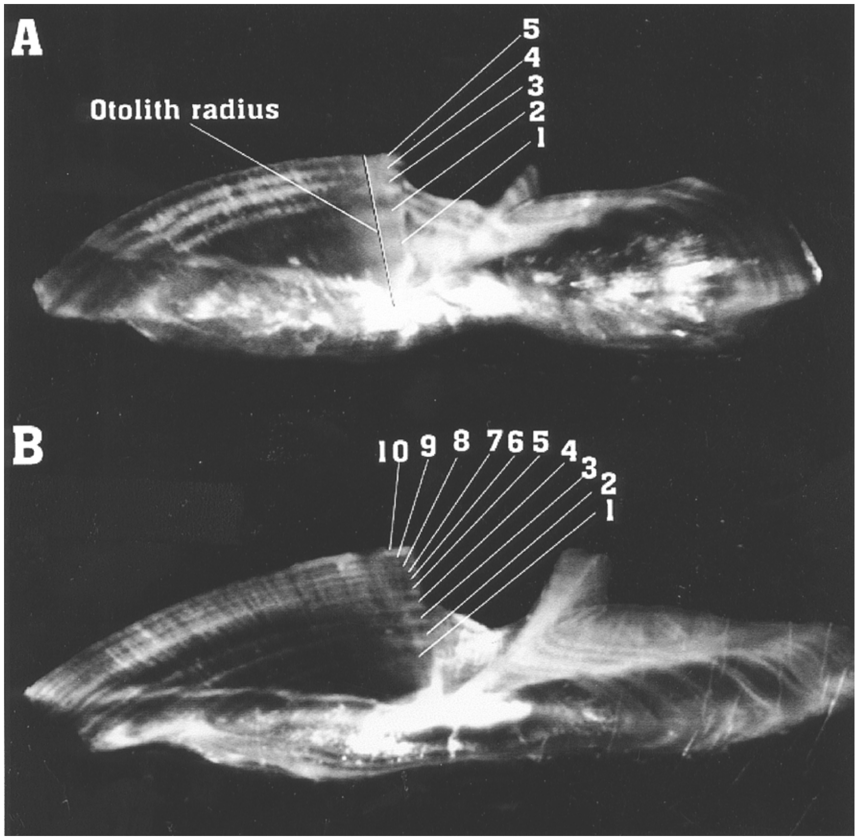

Figure 1

Sectioned sagittae from (**A**) a 5-year-old (345-mm-TL) and (**B**) a 10-year-old (485-mm-TL) eastern Gulf of Mexico red porgy. The 5-year-old fish was caught in September 1996, and the 10-year-old fish was caught in April 1996.

readers was high (86%) for the second readings, one reader read the remaining otoliths to determine age. Each of the remaining otolith sections was read three times, and annulus counts were accepted for ages only if at least two of the three separate readings were the same. Age was considered to be the count with the highest frequency of occurrence. To validate annulus periodicity, marginal increments and their medians were plotted by month for each age and compared for consistent temporal patterns.

Age in years was estimated as the number of opaque rings; therefore, length at age included any growth that occurred after the last opaque ring was formed. Length at age between sampling sources was compared by using an unbalanced two-way analysis of variance (SAS Institute, Inc., 1985). Mean observed length at age was calculated for males, females, and for all aged fish. Age and length data were fitted to a von Bertalanffy growth model with nonlinear regression (SAS Institute, Inc., 1985). We calculated an adjusted r^2 for the resulting curve by using methods described by Helland (1987).

We used age-frequency data from this study to estimate mortality rates from Florida commercial and recreational length data for Florida. Because the number of red porgy measured by the Trip Interview Program[6] and MRFSS[3] were low, we pooled the data from the most recent years for which data were available. Length data from commercial landings were obtained from the TIP[6] from 1992 to 1994 and in 1996. Length data from recreational landings were obtained from the MRFSS[3] and the National Marine Fisheries Service's Headboat Survey[7] and were pooled for years 1990–1996. Because red porgies are protogynous hermaphrodites, we pooled sexed and unsexed fish to generate the catch curves. Instantaneous mortality and survivorship rates were estimated by the Chapman-Robson method (Youngs and Robson, 1978). Age at full recruitment was estimated from the catch curve as being one year older than the age with the greatest catch.

[6] Trip Interview Program (TIP). 1997. Unpubl. data. Florida Fish and Wildlife Conservation Commission, 100 Eigth Avenue, SE, St. Petersburg, FL 33701-5095.

[7] National Marine Fisheries Service Headboat Survey. 1999. Unpubl. data. Beaufort Laboratory, 101 Pivers Island Rd., Beaufort, NC 28516-9722.

Reproduction

Reproductive analyses were based on gonad weights and a histological examination of gonadal tissue. Fish sampled were put on ice soon after capture, and we sampled fish within 36 hours after their capture by the recreational fishery and 10 days after their capture by the commercial fishery. Whole gonads were weighed to the nearest 0.1 g. Some fish were gutted before they were landed. If a portion of gonad was present, it was removed for histological preparation; if none was present, the sex of the fish was listed as unknown. Gonads were fixed in 10% buffered formalin for approximately one week, rinsed in water, and then transferred to 70% ethanol. We removed a sample of tissue from the middle of the preserved gonad and embedded it in paraffin. Several 5.0-µm sections were serially cut from the sample, stained with Harris's haematoxylin, counterstained with eosin (Humason, 1972), and examined under a compound microscope to determine sex and developmental state of the gonads. For ovaries, we staged oocytes as being primary growth, cortical alveoli, or vitellogenic oocytes, or as mature oocytes by using criteria developed by Moe (1969), Wallace and Selman (1981), and West (1990). The frequency of occurrence of oocyte developmental stages (including atretic bodies and postovulatory follicles) was tabulated for approximately 300 oocytes from each ovary by using a computer-driven data-acquisition software package (Optimas Corp., 1996). Mature ovaries were distinguished from immature ovaries by the presence of atretic bodies, advanced oocyte development stages (vitellogenic or mature oocytes), or both. Testes were assigned to development classes (Table 1) by using a modified classification scheme developed from Hyder (1969) and Moe (1969). Transitional males (individuals with gonads in transition from ovaries to testes) were identified according to the criteria of Sadovy and Shapiro (1987).

Sex ratios for all sexed fish were compared for significant differences from 1:1 by using the chi-square test (Snedecor and Cochran, 1971). The length and age at which 50% of the population consisted of males was estimated by fitting a logistic curve to length and age data with sex as a binary response equal to zero for females and to one for males. The curves were fitted to the data by using nonlinear regression (Jandel Corp., 1992).

Reproductive seasonality was determined by examining the monthly changes in gonad stages, the monthly distribution of oocyte stages, and the monthly changes in the gonosomatic index (GSI). The GSI was calculated by using the following equation:

$$GSI = gonad\ weight/(whole\ weight - gonad\ weight).$$

Table 1
Development classes for testes of red porgy.

Classes	Testes
Transitional	Massive atresia of oocytes. Spermatogonia, spermatocytes, and (or) spermatids developing in lumen of testicular lumen. Tailed sperm may be present.
Resting	Mostly spermatogonia and spermatocytes present in the central lobules. Free spermatozoa in the lumen of the lobule, and brown bodies (Grier, 1987) may be present.
Developing	Mostly spermatocytes and spermatids present in the central lobules, free spermatozoa in the lumen of the lobule.
Ripe	Mostly spermatozoa found in the central lobules and in the lumen of the lobule; all or later stages of spermatogenesis occurring in the peripheral lobules.
Spent	Few free spermatozoa in the lumen of the lobule; early stages of spermatogenesis in the peripheral lobules.

Results

Collections

We sampled 877 red porgy that ranged from 194 to 489 mm in length. Although we did not record the locations where fishermen caught their fish, most fishing effort was directed in the Florida Middle Ground and off west central Florida. Most fish (92%) were in length classes between 251 and 400 mm long and had a modal length class of 326–350 mm (Fig. 2). Relationships between lengths, between whole weight and gutted weight, and between TL and weight are shown in Table 2. Male and female data were pooled for the weight-length relationship because sex-specific regression equations were not significantly different (ANCOVA, $P>0.05$). Most of the fish sampled were from the recreational fishery ($n=601$), and they ranged in length from 205 to 455 mm (Fig. 2). Fish from the commercial fishery ($n=276$) ranged from 265 to 489 mm (Fig. 2). The mean length of recreationally caught fish (321 mm, SE=40) was significantly less than the mean length of commercially caught fish (350 mm, SE=40; t-test, $P<0.001$). The length-frequency distributions for commercially and recreationally caught fish were significantly different ($D=0.287$, $P<0.001$). Males ($n=331$) ranged in length from 248 to 470 mm and females ($n=456$) from 205 to 455 mm (Table 3). The mean length of males (341 mm, SE=36.3) was significantly greater than that of females (316.2 mm, SE=40.5; t-test, $P<0.001$). The length-frequency distributions for males and females were significantly different ($D=0.317$, $P<0.001$). The largest fish examined (489 mm) had been gutted; therefore the sex of the specimen was unknown.

Age, growth, and mortality

Under reflected light, alternating opaque (white) and translucent (dark) zones were evident in red porgy otoliths (Fig. 1). Two readers examined a subsample of 241 otoliths, and 50% of their readings were in agreement. Most of the disagreements (71%) differed by only one

Table 2

The linear relationships among lengths, among weights, and between weight and length, and the logistic proportion of males by age and total length for red porgy from the eastern Gulf of Mexico. SL = standard length (mm), FL = fork length (mm), TL = total length (mm), WT = whole weight (gm), GWT = gutted weight (gm). n = the number of fish sampled, and the standard error is given in parentheses.

Y	*X*	*n*	*a*	*b*	r^2
			$Y = a + bX$		
SL	*FL*	876	–5.3 (1.4)	0.89 (0.005)	0.97
SL	*TL*	869	–10.1 (1.6)	0.78 (0.005)	0.97
FL	*SL*	876	13.0 (1.5)	1.09 (0.005)	0.97
FL	*TL*	867	–4.9 (1.0)	0.87 (0.003)	0.99
TL	*SL*	869	24.5 (2.0)	1.24 (0.01)	0.97
TL	*FL*	867	8.9 (1.1)	1.13 (0.004)	0.99
WT	*GWT*	121	6.0 (3.4)	1.05 (0.008)	0.99
$\log_{10}WT$	$\log_{10}TL$	572	–4.51 (0.053)	2.86 (0.216)	0.97
$\log_{10}GWT$	$\log_{10}TL$	272	–4.45 (0.08)	2.82 (0.32)	0.97
			$Y = 1/(1+e^{(a(x-b))})$		
Proportion male	*Age*	781	–0.703 (0.067)	5.332 (0.118)	
Proportion male	*TL*	784	–0.017 (0.002)	345.5 (5.1)	

zone. A second independent reading of the subsample by both readers resulted in a higher agreement rate of 86% and indicated that both readers were consistently identifying the same features as opaque zones. Of 877 sectioned otoliths examined, 852 (97%) could be assigned ages. Of the otoliths that could be aged, measurements for marginal-increment analyses could not be made for 40 (4.6%) because of broken or occluded areas along the otolith radius.

Analyses of marginal-increment data for fish ages 2–10 yr suggested that opaque zones were formed once a year during the late spring to early summer (Fig. 3). Because of small sample sizes, we pooled marginal-increment data for ages 8 to 10. During the spring and early summer, the widest increments (ring formation was imminent) and the narrowest increments (ring formation was just completed) were present, indicating that rings were being formed during this period. In addition, monthly median marginal increments for ages 2–10 had a consistent yearly pattern of high median values from October to April and low values from June to August (Fig. 3).

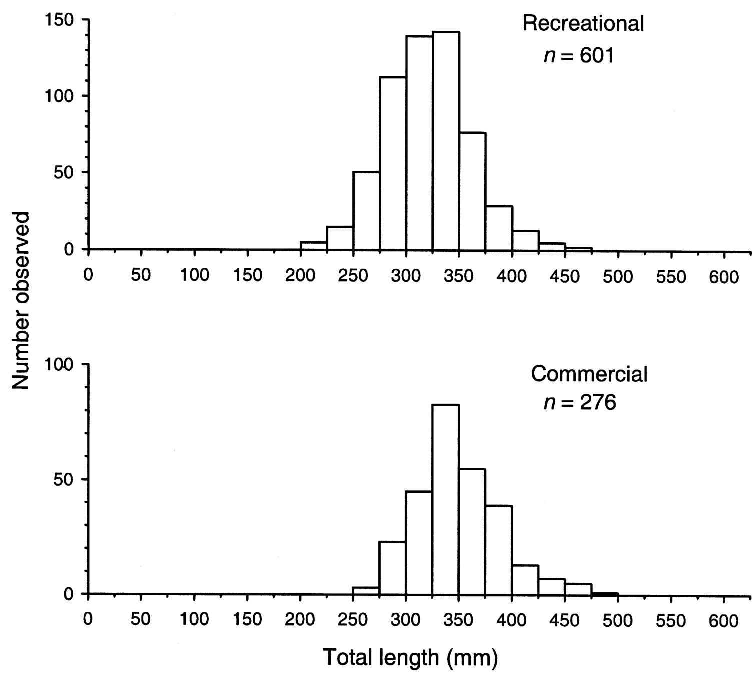

Figure 2

Total lengths of red porgy from the eastern Gulf of Mexico by sampling source.

Ages ranged from 1 to 17 years and most fish (83%) were between ages 3 and 8. No females older than 10 years were observed. Initial growth of red porgy was rapid, and fish attained a mean length of 260 mm during their second year (age 1; Table 4). Subsequent increases in length, however, were low (<40 mm/yr). Average lengths at age were not significantly different between males and females ($F_{8,741}$=1.5, P=0.155) or between sampling sources ($F_{8,817}$=0.96, P=0.462). The estimated von Bertalanffy growth parameters (standard error) for all aged fish (n=854) were L_{∞}=459(31) mm, K=0.111 (0.028)/yr, and t_0=–6.6 (1.3) yr. Predicted lengths at age were similar to mean lengths at age (Table 4, Fig. 4). The adjusted r^2 for the growth model was 0.40.

Fishery-based length-frequency data were transformed into age frequencies by using age- length keys constructed from the ages of the fish in our study. Full recruitment into both the recreational and commercial fisheries occurred at age 4. Survivorship (standard error) of red porgy was estimated to be 0.42(0.001) from the headboat fishery data, 0.54(0.046) from the recreational fishery data and 0.58(0.014) from the commercial fishery data. Instantaneous mortality estimates (Z=–ln survivorship) were 0.87

Table 3

Number of males, number of females, and percentage of male red porgy in relation to the total number of sexed individuals by length and age from the eastern Gulf of Mexico.

Length (mm TL)	No. of females	No. of males	% males	Age (yr)	No. of females	No. of males	% males
<200	1	—	—	1	6	1	14.29
201–225	4	—	—	2	55	5	8.33
226–250	14	1	6.67	3	100	20	16.67
251–375	48	6	11.11	4	124	38	23.46
276–300	98	37	27.41	5	89	89	50.00
301–325	113	60	34.68	6	49	63	56.25
326–350	95	113	54.33	7	15	64	81.01
351–375	46	63	57.80	8	6	28	82.35
376–400	22	29	56.86	9	2	9	81.82
401–400	7	16	69.57	10	3	10	76.92
426–450	3	5	62.50	11+		5	100
451–475	2	1	33.33				

Table 4

Mean empirical and predicted total lengths (mm TL) of female, male, and all red porgy sampled from the eastern Gulf of Mexico. Standard error is given in parentheses, and n = number of fish examined.

	Female			Male			All fish			
Age (yr)	n	Mean empirical	Range	n	Mean empirical	Range	n	Mean empirical	Range	Predicted
1	6	253 (36.7)	194–290	1	298	—	7	260 (37.4)	194–298	262
2	55	292 (31.8)	205–363	5	311 (40.9)	285–382	61	294 (32.6)	205–382	283
3	99	288 (29.1)	230–368	20	300 (28.9)	248–350	124	291 (31.2)	220–378	302
4	122	315 (29.9)	245–402	38	318 (30.0)	258–372	171	316 (29.7)	245–402	318
5	88	337 (36.5)	265–455	87	337 (32.4)	276–435	189	339 (34.8)	265–455	333
6	48	344 (25.3)	290–405	63	346 (26.1)	300–420	134	348 (26.9)	290–426	347
7	15	360 (21.9)	330–397	62	351 (32.0)	288–425	88	357 (33.3)	288–489	358
8	6	364 (33.1)	326–415	27	340 (20.2)	295–380	38	348 (27.0)	295–425	369
9	2	410 (46.0)	377–442	9	379 (36.7)	330–450	13	388 (40.0)	330–452	379
10	3	379 (39.6)	334–407	9	407 (38.5)	348–470	18	396 (46.5)	321–470	387
11				1	405	—	4	415 (20.9)	390–436	395
12				1	397	—	2	393 (5.7)	389–397	402
13				1	393	—	1	393	—	408
14				1	389	—	2	377 (17.7)	364–389	413
15							1	445	—	418
17				1	438	—	1	438	—	426

for the headboat fishery, 0.62 for the recreational fishery, and 0.54 for the commercial fishery.

Reproduction

Red porgy are protogynous hermaphrodites. We classified 68 males (8% of the sexed fish) as transitional-sex-stage fish because of the simultaneous presence of deteriorating ovarian tissue and proliferating male tissue. We determined that the gonadal structure was delimited (Sadovy and Shapiro, 1987) because connective tissue separated testicular from ovarian tissue. Sex ratios and length and age data were consistent with monandric protogyny. The overall sex ratio of males to females was 1.0:1.6, which was significantly different from 1:1, χ^2=51.0, df=1, P<0.001). In addition, the modal length class and age of females (301–325 mm; 4 yr) were less than the modal length class and age of males (326–350 mm; 5 yr; Table 3). We also did not observe any males less than 298 mm, whereas the smallest female was 194 mm. The estimated age and length at which 50% of fish in our samples were males were 5.3 years and 345.5 mm (Table 2).

Few immature female (n=10) red porgies were observed in our samples. We did not find any age-1 (n=6) immature female red porgy, and most age-2 (91%, n=55) and age-3 (96%, n=99) females were sexually mature. All females age 4 or older were sexually mature. Immature females ranged in length from 194 to 302 mm and the smallest mature female was 230 mm. More than half (69%) of the fish observed were mature by the length class 226–250 mm (n=17).

Red porgy in the eastern GOM spawn from December to April. During this time period, ovaries containing either mature oocytes (spawning is imminent) or postovulatory follicles (spawning has recently occurred) were observed (Fig. 5). Throughout the rest of the year, ovaries progressed from containing only primary growth oocytes (May to August) to containing cortical alveoli and vitellogenic oocytes (September to November; Fig. 5). Ripe males were observed in every month except July and September (Fig. 6). Immature (transitional-sex-stage) males were captured throughout most of the year, but they were absent or rare just prior to and during the spawning season (November to April). For both sexes, median GSI's were low from May to October (<0.015 for females and <0.005 for males; Fig. 7). In January, median GSI's increased dramatically (0.035 for females and 0.019 for males) and then gradually decreased through August.

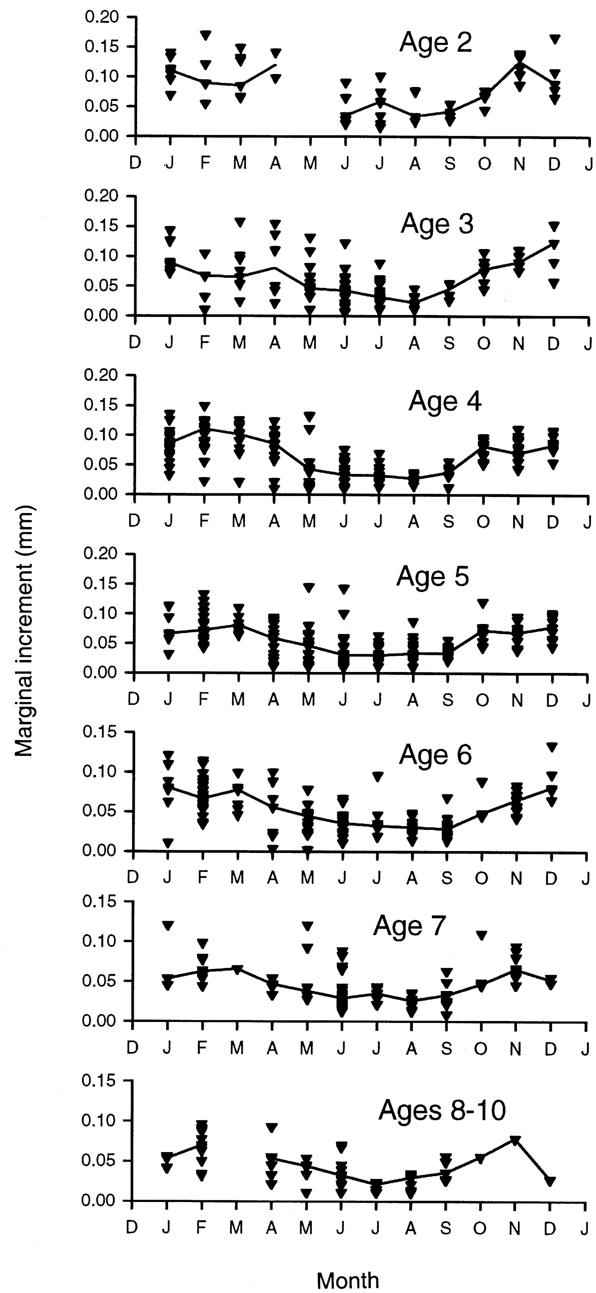

Figure 3

Marginal increments from sectioned otoliths of red porgy ages 2–10 years from the eastern Gulf of Mexico. Median monthly increments are identified by the solid line. Because of low sample sizes, ages 8–10 were pooled.

Discussion

Collections

There appeared to be a trend towards smaller red porgy in the GOM from the 1980s to the 1990s. Although landings have not increased since the early 1980s (Gulf-wide average annual landings of approximately 250,000 lbs; [Goodyear and Thompson[1]]), the length structure of the population has changed. Between 1990 and 1992, modal lengths of commercially caught fish have decreased from 357 mm to 279 mm for fish landed in Florida and from 381 mm to 254 mm for fish landed in Louisiana and Texas (Goodyear and Thompson[1]). In addition, there has been a decline from 508 mm to 381 mm in the maximum length of fish caught from headboats during 1979–91 (Goodyear and

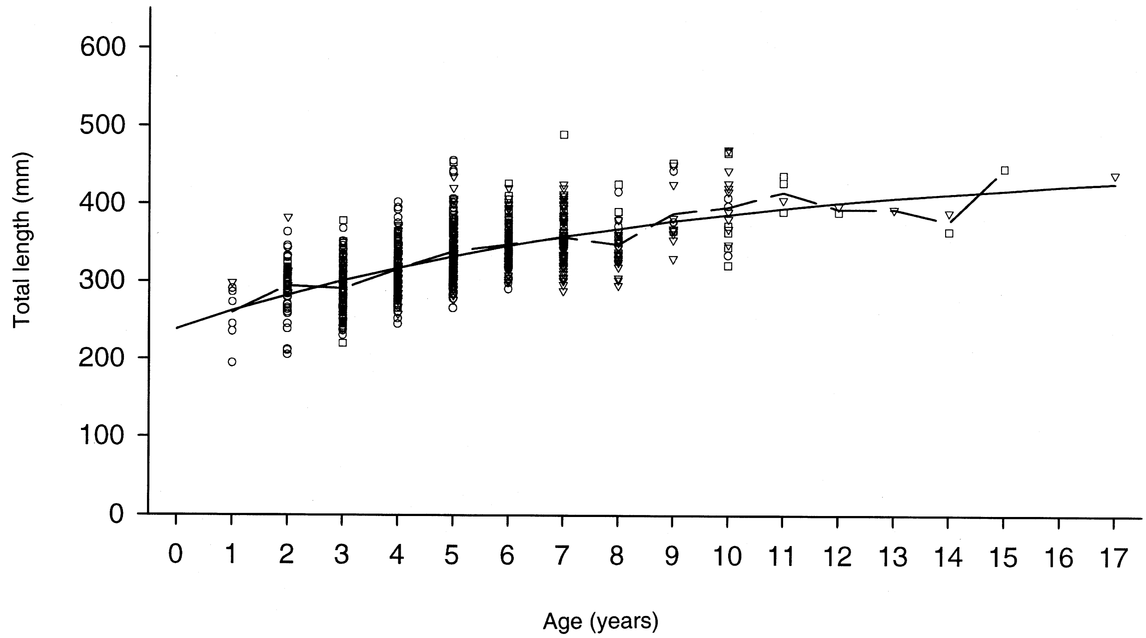

Figure 4

Total length at age, mean length at age (dashed line), and predicted length at age (solid line) of red porgy from the eastern Gulf of Mexico. Circles=females, triangles=males, and squares=unknown sex.

Thompson[1]). These trends may reflect differences between the modal length class (326–350 mm) of fish we sampled from the eastern GOM and earlier collections (349–404 mm[8]) from the Flower Garden Banks off Texas by Nelson (1988). However, because we did not obtain specific depth and gear information for fish we sampled, we cannot discount these factors to explain differences between our samples and Nelson's (1988). Decreases in average and modal lengths for red porgy in the SAB have been associated with increased fishing pressure (Collins and Sedberry, 1991; Harris and McGovern, 1997; Vaughan[5]).

Age, growth, and mortality

Although scales and otoliths have been used to determine the ages of red porgy, which structure is used, as well as how it is prepared, affects ring interpretation. Although we did not use scales to age red porgy, comparisons of ring counts determined from scales and whole otoliths from the same fish have had between 80% and 90% agreement rates (Manooch and Huntsman, 1977; Machias et al., 1998). However, Manooch and Huntsman (1977) cautioned that as age increases, both scales and whole otoliths become more difficult to interpret because the rings at the outer edge become difficult to discern. We used sectioned red porgy otoliths because most studies that have compared aging structures have found that sectioned otoliths provide more reliable estimates of age than either scales or whole otoliths, particularly for older fish (e.g. Beamish and McFarlane, 1983; Collins et al., 1987; Lowerre-Barbieri et al., 1994; Crabtree et al., 1996; Taylor et al.[9]). Sectioning otoliths also increases readability rates; Pajuelo and Lorenzo (1996) and our study were able to assign ages to 81% and 97% of the otoliths, respectively. Whole otoliths and scales used to age red porgy have provided mixed success in assigning ages to fish (54–90%: Manooch and Huntsman, 1977; Nelson, 1988; Vassilopoulou and Papaconstantinou, 1992; Harris and McGovern, 1997; Machias et al., 1998).

Opaque zones in red porgy otoliths appear to be formed annually. From marginal-increment analyses, we found that GOM red porgy form one opaque zone per year in the late spring and summer. Marginal-increment analysis has also been used by others to validate annual zone deposition in aging structures (Manooch and Huntsman, 1977; Nelson, 1988; Pajuelo and Lorenzo, 1996). Additionally, Machias et al. (1998) reported that red porgy from the Mediterranean Sea held in ponds for known periods of time formed annual rings in both scales and otoliths, and Collins et al. (1996) recaptured one oxytetracycline-injected red porgy (released in the SAB) in which the loca-

[8] Reported lengths were transformed from FL to TL by using the equation from Table 2.

[9] Taylor, R. G., J. A. Whittington, H. J. Grier, and R. E. Crabtree. In prep. Age, growth, maturation, and protandric sex reversal in the common snook, *Centropomus undecimalis*, from South Florida waters. Florida Department of Environmental Protection, 100 Eigth Avenue SE, St. Petersburg, FL 33701-5095.

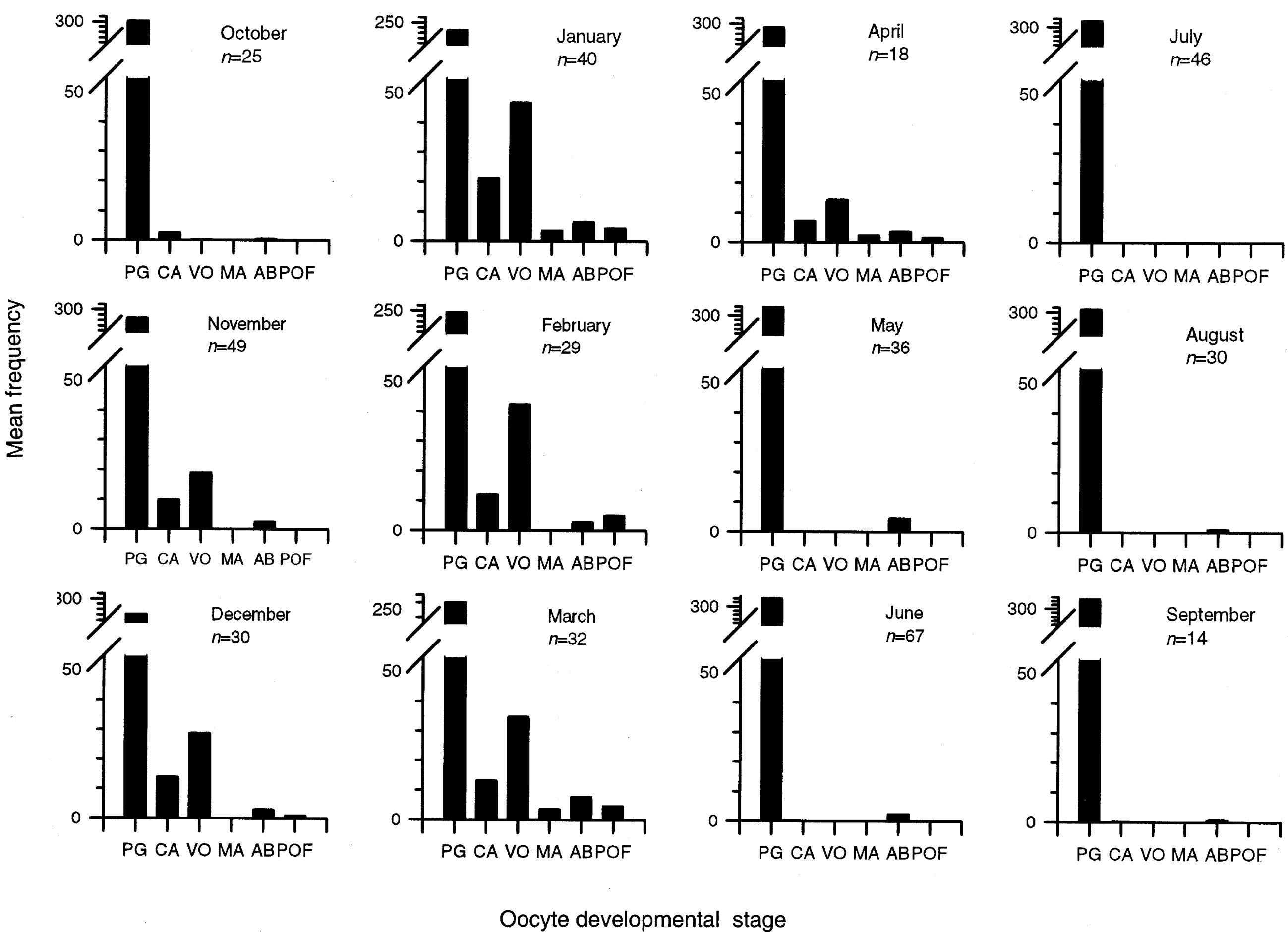

Figure 5

Average frequency of occurrence of oocyte developmental stages by month for red porgy from the eastern Gulf of Mexico. PG = primary growth oocyte, CA = cortical alveolar oocyte, VO = vitellogenic oocyte, MA = mature oocyte, AB = atretic body, and POF = postovulatory follicle.

tion of the oxytetracycline mark was consistent with the annual formation of the opaque zone.

We confirmed that red porgy are moderately long-lived fish (Manooch and Hassler, 1978). The oldest individual we aged was 17 years old, a year younger than the sectioned-otolith-based maximum age of 18 years reported for red porgy in the SAB (Vaughan[5]). Nelson (1988) reported the maximum scale-based age for this species in the GOM was 6 years and suggested that the reason for the lower maximum age than that found in the SAB (15 years by Manooch and Huntsman, 1977) was that older fish had been eliminated through higher rates of mortality. He reported that mortality rates in the western GOM (Z=0.86/yr) were much higher than those in the SAB (Z=0.44/yr; Manooch and Huntsman, 1977). However, this argument is circular because Nelson (1988) estimated mortality from catch curves that had been based on the age structure of the fish he sampled. If his age distribution was truncated owing to sampling or aging bias, then his estimates of mortality would have been higher than the true rate. Nelson's (1988) sample size was small (n=126) and geographically restricted (Flower Garden Banks off Texas) compared with the sample size of Manooch and Huntsman (1977), which was large (n=1777) and from a broad geographic region (SAB).

Our observed and predicted lengths at age were lower than those reported by Nelson (1988) for the Flower Garden off Texas. It is difficult to assess why our observed and predicted lengths at age were lower, but the limited sample size of Nelson (1988) (n=126) may not be representative of the GOM population. Other factors that may contribute to these differences include regional differences in growth within the GOM, depth of capture, hook size, or biases between the aging structures. However, Goodyear and Thompson[1] reported that the depths where red porgy were most commonly captured by GOM fisheries overlapped the depth range in which most of the fish sampled by Nelson (1988) were captured (60–90 m). Hook size

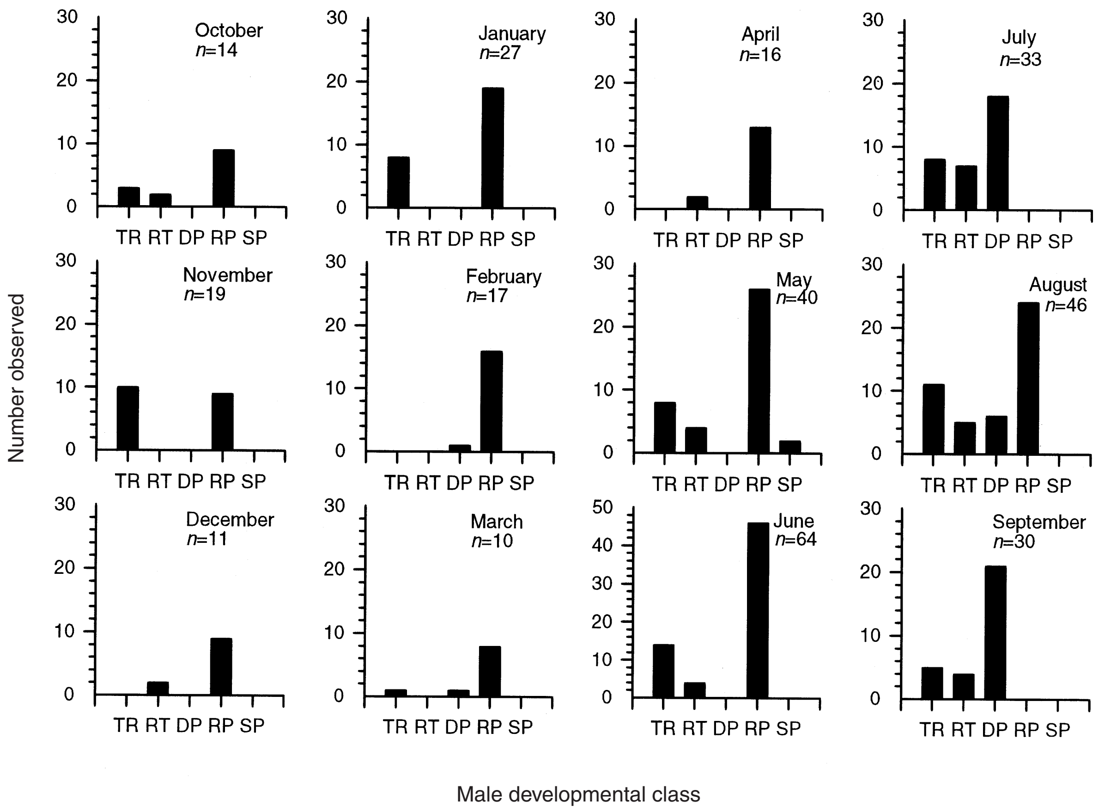

Figure 6

Frequency of occurrence of male developmental classes by month for red porgy from the eastern Gulf of Mexico. TR = transitional, RT = resting, DP = developing, RP = ripe, SP=spent

may have had a limited effect on size differences because the mean lengths at age of fish we sampled that were caught with commercial or recreational gear were not significantly different, and Nelson (1988) reported that the hook sizes did not seem to affect the size distributions of several fish species captured in his study. Finally, biases usually associated with aging structures occur at older ages when rings crowd together at the scale edge and are harder to interpret. Manooch and Huntsman (1977) were able to use scales to age red porgy to 15 years, a much greater age than the maximum age of 6 years reported by Nelson (1988). Therefore, Nelson's estimated ages may accurately describe the ages of the fish he sampled.

Changes in the average length at age between the early 1980s and present may also be the result of size-selective fishing over time, i.e. if larger fish were more vulnerable to capture, then faster-growing fish within an age class would be selectively removed from the population and the result would be a reduced mean size at age for older age classes and an underestimated L_∞ (Ricker, 1969; Pitcher and Hart, 1982). We could not demonstrate size-selective fishing pressure, but there was a shift in the size structure of red porgy stocks in the GOM towards smaller fish (Goodyear and Thompson[1])—a shift that suggests that fishing pressure is affecting the size structure of the stock.

For SAB red porgy stocks, Harris and McGovern (1997) have suggested that size-selective fishing and increases in fishing mortality have caused a decrease in mean lengths at age and L_∞ in SAB red porgy stocks. The average lengths at age 6 years decreased from 451 mm in 1972–74 (Manooch and Huntsman, 1977) to 363 mm[8] in 1991–94 (Harris and McGovern, 1997), and estimated L_∞ decreased from 763 mm and 528 mm[8] for 1972–74 (Manooch and Huntsman, 1977; Harris and McGovern, 1997) to 412 mm[8] for 1991–94 (Harris and McGovern, 1997). Although differences in sampling source (fishery dependent vs. fishery independent) between Manooch and Huntsman (1977) and Harris and McGovern (1997) may have accounted for the observed differences, Harris and McGovern (1997) noted that the same changes occurred from 1979 to 1994 in their fishery-independent samples. Similar trends have been reported for vermilion snapper (*Rhomboplites aurorubens*) in the GOM (Hood and Johnson, 1999) and in the SAB (Zhao et al., 1997), which are a part of the same fishery as red porgy. However, for the SAB, Potts et al. (1998) suggested that differences in gear types may have accounted for differences in length at age reported by Zhao et al. (1997).

Red porgy were fully recruited into the GOM recreational and commercial fisheries by age 4. This is the same age that red porgy in the Flower Garden Banks were fully recruited to the sampling gear (primarily hook-and-line) used by Nelson (1988). In the SAB, the age of full recruitment decreased from age 5 in 1972–83 to age 4 in 1984–86, probably because of higher exploitation rates (Vaughan et al., 1992). Huntsman et al. (1983) reported that the age of full recruitment to the SAB head boat fishery was 4.1–4.3 years.

Our estimates of Z (0.54–0.87/yr) are within the range of reported estimates for other populations sustaining fishing pressure. Nelson (1988) estimated Z to be 0.86/yr for fish from the Flower Garden Banks off Texas in 1980–82. In the SAB, estimates of Z increased from the early 1970s through the early 1990s: Z = 0.64/yr for SAB populations from 1972 to 1974 (Manooch and Huntsman, 1977) to Z = 1.58/yr for 1991 (Huntsman et al.[10]). Recently, Vaughan[5] estimated Z for the SAB to be between 0.90 to 0.94/yr depending on the input value of natural mortality in his stock assessment model. Vassilopoulou and Papaconstantinou (1992) reported Z = 0.34/yr for a relatively unexploited red porgy stock in the Mediterranean Sea and estimated natural mortality to be 0.28/yr.

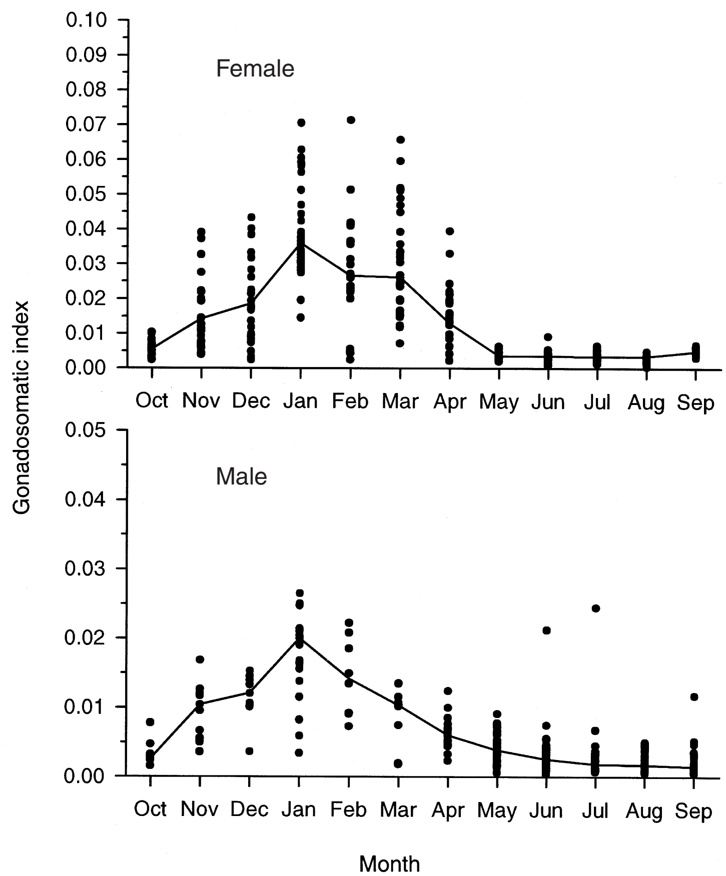

Figure 7

Monthly gonadosomatic indices (GSI) for female and male red porgy from the eastern Gulf of Mexico. Median values are connected by the solid line.

Reproduction

Protogynous hermaphrodites such as red porgy may be more susceptible to overfishing than gonochoristic species if size-selective fishing reduces the number of males available for spawning (Bannerot et al., 1987; Koenig et al., 1996). This trend is not evident for GOM red porgy. Our sex ratio of 1:1.6 had proportionally fewer females than did the 1:2.8 ratio reported by Nelson (1988) for 1980–82. In the SAB, the proportion of females has been increasing in association with fishing pressure. Manooch (1976) estimated that the sex ratio of red porgy in the SAB was 1:2.8 for 1972–74 and that proportionally more males were landed in the fishery than during later years (1:4.9–1:6.5 for 1979–1994; Harris and McGovern, 1997). The sex ratio of another GOM protogynous hermaphroditic reef-fish species, the gag (*Mycteroperca microlepis*), has been affected by overfishing (Koenig et al. 1996) in that there are proportionally fewer male gag in overfished populations than in less fished populations (male-to-female ratio of 1:76.6 for 1991–93 (Koenig et al., 1996) compared with 1:4.9 for 1977–80 [Hood and Schleider, 1992]). Koenig et al. (1996) hypothesized that because males are more aggressive in feeding, they are more likely to be captured by fishermen who target gag aggregations.

Our reported lengths at maturity (most red porgy were mature by 225 mm) were closer to lengths reported for exploited populations (<275 mm; Pajuelo and Lorenzo, 1996; Harris and McGovern, 1997) than for lightly or newly exploited populations (>276 mm; Manooch, 1976; Vassilopoulou and Papaconstantinou, 1992; Harris and McGovern, 1997). Decreases in the size at maturity for red porgy may be associated with increased fishing effort; Harris and McGovern (1997) found 27% of red porgy females were mature between 251 and 275 mm in pooled years 1979–81 compared with 54% in pooled years 1991–94.

Sexual transition occurred at smaller sizes than those reported by Nelson (1988): our estimated length at which half the population is male was 345 mm compared with 404 mm.[8] In the SAB, Harris and McGovern (1997) reported an increasing proportion of males between 351 and 400 mm over time, 12.13% in 1979–81, 32.35% in 1988–90, and 49.33% in 1991–94, which they attributed to size-selective fishing pressure. For most protogynous reef-fish

[10] Huntsman, G. R., D. S. Vaughn, and J. C. Potts. 1993. Trends in population status of the red porgy *Pagrus pagrus* in the Atlantic Ocean of North Carolina and South Carolina, USA, 1971–1992. South Atlantic Fishery Management Council, 1 South Park Circle, Charleston, SC 29422-1997.

species, the removal of males causes females to change sex (Sadovy and Shapiro, 1987). Therefore, the removal of larger fish (males) by fisheries causes smaller and smaller females to change sex and results in an increase in the proportion of smaller-size males.

Based on monthly changes in the percentage of fish in the various maturity classes, the frequencies of different oocyte stages, and GSI, we believe that red porgy spawn in the GOM from January to April. Our findings are consistent with spawning season observations reported for red porgy in the GOM by Nelson (1988), in the SAB by Manooch (1976), in the Canary Islands by Pajuelo and Lorenzo (1996), and in the Mediterranean Sea by Vassilopoulou (1989) and Vassilopoulou and Papaconstantinou (1992).

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